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FACTORS CONTROLLING GROWTH OF POND PINE SEEDLINGS IN ORGANIC SOILS OF THE CAROLINAS

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INTRODUCTION

THE POND PINE HABITAT

The pond pine, *Pinus serotina* Michx., occurs in both wet and dry habitats throughout the Southeastern Coastal Plain from New Jersey to southern Alabama. In the Carolinas it is most abundant on peat lands, where it forms an open tree canopy above a dense shrub layer. This combination of peat soil, dense shrubs and a pond pine tree canopy is known botanically and colloquially as "pocosin" and the pond pine is frequently called the "pocosin pine."

Pocosins are characterized by extremes. The peat surface soils are very acid and may be flooded to a depth of several inches for long periods. Fire occurs at intervals seldom greater than 15 to 20 years and may burn both the vegetation and the surface soil. The pocosin pine is well adapted to these conditions, since it survives long periods of flooding and sprouts vigorously from the trunk or root crown after fire. Its serotine cones open after fire and stands of this tree therefore are commonly uneven aged. Although the tree is slow-growing in pocosins and the upper stem is often crooked because of sprouting after fires, the pond pine is the principal commercial species of extensive lowlands throughout the Coastal Plain.

Increasing demands for timber in recent years have emphasized the need for improving timber yields from pond pine lowlands. Because flooding has been generally accepted as the principal factor limiting tree growth in pocosins, drainage has frequently been the only silvicultural technique employed. The effects of drainage on rates of tree growth have been variable, indicating that other factors are sometimes important.

Recent phytosociological evidence also indicates that factors in addition to flooding may limit tree growth rates in pocosins (Woodwell 1956). According to this study sites subject to apparently similar flooding regimes and displaying similar soil profiles differ in site quality and these variations are in some degree correlated with the floristic composition and physiognomy of the vegetation. The present study was undertaken to discover experimentally those factors, other than flooding, which are important in determining differences in both the vegetation and site quality of pocosins.

Research was supported by a grant from the International Paper Company. Stands selected for study were on lands of that company. Experiments were carried out in the Department of Botany and in the School of Forestry, Duke University. Appreciation is due Professor H. J. Oosting, who directed the study, and Professors C. W. Ralston and F. X. Schumacher for help with soils and statistics, respectively.

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Topography and Vegetation Associated with Pocosins

Geologists agree in general that the surface sediments of that section of the Coastal Plain less than 60 ft. above sea level are of Pleistocene marine origin (Richards 1950). Topography of these lands is characterized by low sand ridges which rise only a few feet above the level of long-term flooding of the swamps. Vegetation of the ridges is usually the Pinus palustris/Aristida community; that of the swamps, the Nyssa-Taxodium/Magnolia/Lyonia community (Woodwell 1956). Between the sand ridges but higher than the swamps are extensive flatlands which do not have surface drainage channels. These flatlands support the pocosins of the present study.

The pocosin flatlands are of 3 physiographic types. Pocosins occur in the numerous shallow elliptical depressions called "Carolina Bays," which are common throughout the Coastal Plain of the Carolinas. Certain extensive poorly drained flatlands of irregular outline also support pocosins. In addition, pocosins occur in the depressions between closely spaced sand ridges, thereby forming part of the topography locally called "ridge and bay." Ridge and bay is particularly common in the coastal sections of South Carolina.

Literature on Pocosins and the Fertility of Organic Soils for Pine

Based on sampling data from 56 pocosins in the Carolinas, Woodwell (1956) recognized 3 pocosin communities, distinguished by the species of the shrub layer. A tree union, the *Pinus serotina* union, occurs in all pocosins. A shrub union, dominated by *Cyrilla racemiflora* L., occurs in North Carolina and is replaced southward by a union dominated by *Lyonia lucida* (Lam.) K. Koch. Throughout the ranges of these unions a third union, characterized by the presence of *Zenobia pulverulenta* (Bartr.) Pollard, among several other species, is common. The plant communities were named after the unions as the Pinus/Cyrilla, Pinus/Lyonia and Pinus/Zenobia communities.

Woodwell cites evidence to show that the Zenobia union is usually succeeded by either the Cyrilla or Lyonia unions, although the Zenobia union is long lived on poor sites. No obvious correlation between either soil profile or flooding and the shrub unions was noted and he concluded that unknown soil characteristics in addition to flooding and soil profile are important in determining both the vegetation and site quality.

Other studies have contributed evidence supporting this conclusion. Drainage of organic soils by pulp companies of the Southeast increased the growth rates of trees on certain sites but on others no noticeable change occurred in either tree growth rates or in the vegetation even after several years. Wells & Shunk (1928) noted that there had been no change in the vegetation of a grass-sedge bog near Burgaw, North Carolina within 7 yrs after drainage. They concluded that some "toxic" property of the soil remains after drainage, although they were unable to demonstrate this toxicity experimentally. Dachnowski-Stokes & Wells (1929) came to a similar conclusion after a study of a pocosin in Carteret County, North Carolina. There has, however, been no definitive study of this "toxic" quality with specific reference to the organic soils of the coastal plain of the Carolinas. In the instances cited "toxicity" seems to have been used with reference to lingering bog conditions subsequent to drainage. Presumably these lingering conditions are not the direct effects of flooding on the vegetation but rather some quality of the soil itself. This quality might be either physical, chemical or biological and still fall within the very broad meaning of "toxicity" as used in earlier studies.

Physical factors affecting plant growth might be such soil characteristics as density, organic matter content, pore space and moisture retention. Chemical factors influencing growth might be either differences in nutrient availability or the presence of toxic quantities of some organic or inorganic substance.

The nutrition of agricultural crops in drained organic soils has been studied extensively. In general organic soils are productive under tillage and contain higher levels of available nutrient elements than mineral soils. Nitrogen and calcium are usually high. Phosphorus and potassium are often low. Deficiencies of the trace elements copper, boron, manganese and zinc have been recognized in tilled organic soils in Florida (Lyon & Buckman 1950). Recently molybdenum deficiency has been recognized as common in acid sands of the Atlantic and Gulf Coasts (E. J. Rubins 1956), and may occur in organic soils as well. No widespread "toxicity" has been discovered in these soils.

The nutrient relationships existing between undisturbed organic soils and the native vegetation are not well known. The relationships are complicated by the occurrence of the nutrient elements in organic complexes and by changes in the relative solubility of the nutrient elements at low pH. Phosphorus, for example, forms insoluble iron and aluminum phosphates in highly acid mineral soils (Lyon & Buckman 1950) and may therefore be unavailable for plant growth. Struthers & Sieling (1950) and Swenson *et al.* (1949) have shown that organic anions such as malate, oxalate and citrate form insoluble iron and aluminum compounds under acid conditions and that these compounds are more stable than iron and aluminum phosphates. Because these organic anions are usually present in organic soils and may render the iron and aluminum inactive, phosphorous may be more readily available for plant growth in these soils than in certain acid mineral soils. In general, however, undisturbed organic soils are characteristically low in available plant nutrients, especially phosphorus, and will not support most crop plants without heavy liming (Russell 1950).

The occurrence in peat of substances toxic to plants has been of interest to botanists for many years.

Waksman (1942) summarizes several of the early papers dealing with the toxicity of peats. None of these studies, however, specifically identifies the toxin. Russell (1950) cites studies which indicate that some of the products of reducing conditions such as hydrogen sulfide are toxic to plants. A series of studies of the Wareham Heath soils in England (Nielson-Jones 1940; Brian *et al.* 1945) indicates that the toxicity of these soils toward trees is due to "gliotoxin," produced by species of *Penicillium*. Brian *et al.* report that gliotoxin is toxic to mycorrhizal fungi and may therefore be the indirect cause of the poor growth of trees on these sites.

Other biological causes of differences in site quality include an almost infinite variety of possible combinations of factors. The microbiology of the soil has been the subject of many studies and usually, when pines have been involved, the presence of mycorrhizal fungi has been associated with an increase in pine growth (Kelley 1950). Soil acidity exerts a high degree of control over the soil microflora, high acidities excluding most bacteria and therefore limiting nitrification (Russell 1950). The competition among higher plants for water and nutrients has been shown by studies such as that of Korstian & Coile (1938) to restrict the growth of pine seedlings.

There have been several descriptive studies made in an effort to correlate various soil characteristics with the growth of pond pine. Coile (1952) found that increased amounts of silt and clay in the subsoil were correlated with increased site index for pond pine. Hofmann (1949) showed that in organic soils site index increases with a decrease in the product of the depth of the A_1 horizon times the organic matter content of this horizon. He found also that site indices of pond pine increased with decreasing organic matter content of the A_1 horizon. This correlation was confirmed by Zahner (1951).

From the literature, therefore, one would expect the acid organic soils of the Coastal Plain to be low in available plant nutrients and to support a microflora dominated by fungi. The possibility of the accumulation of substances toxic to plants or toxic to mycorrhizal fungi exists. Various descriptive studies of the relationships between the rate of tree growth and certain soil characteristics have indicated that the poor site quality is associated with increasing quantities of organic matter in the surface soil.

OBJECTIVE

Previous research has shown that variation in site quality exists among pocosins and that the vegetation is correlated with this variation. In addition there is an increasing amount of evidence indicating that flooding is not the direct cause of differences in site quality among certain pocosins. This evidence indicates that the causes of these differences are characteristics of the organic horizon. The objective of the present work was to discover the factors causing differences in site quality among pocosins.

METHODS

RESEARCH PLAN

Descriptive studies included the selection of 6 sites, measurement of site index and the analyses of the surface soils for chemical and physical characteristics which might influence site quality.

Experimental studies using pine seedlings in soil pot cultures were designed to determine and confirm the specific causes of differences in site quality. In addition, to discover whether the pond pine possesses nutrient requirements particularly well-adapted to the extreme pocosin habitat, comparisons were made of the growth of pond and loblolly pine seedlings in nutrient solutions containing various concentrations of the major elements. In the latter experiment pond pine seeds from two sources were used to show whether physiological variation within the species might influence growth under various conditions.

SAMPLING OF SOILS

The six organic soils were obtained from four pocosins and two swamps. Swamp soils were included for comparison because swamps, unlike pocosins, characteristically occur in natural drainage channels and the fertility of the swamps was therefore expected to be higher than that of the pocosins. One pocosin was selected from a Pinus/Cyrilla community, one from a Pinus/Lyonia, and two from Pinus/-Zenobia communities. According to Woodwell (1956) the former two soils were representative of pocosins of good site quality, while the latter two were representative of sites of poor quality.

Site index was determined from standing trees for each of these sites using the curves of Hofmann (1949) for pond pine and of Coile (1952) for loblolly.

Soil was taken from the surface 6-in. horizon in one locality in each stand. Soils were stored in large air- and moisture-proof plastic bags which were placed in barrels for ease of handling. These samples were used in all the nutrient studies.

DESIGN OF THE NUTRIENT BENCH

Nutrient studies were carried out in the greenhouse in a center bench to obtain as nearly uniform conditions of light and temperature as possible. The bench was divided into compartments 4 in. deep, each carefully fitted with heavy plastic sheeting to make the nutrient tanks. Nutrient solutions were stored in jugs under the bench and supplied to the tanks through tubes arranged to siphon over the edge of the tanks. A small electric air pump supplied sufficient pressure to fill the tanks. Plants were grown in these tanks in plastic containers, perforated at the bottom.

PINE SEED SOURCES

Pond pine seeds were obtained from single trees from two sites which represent extremes of soil conditions as well as different geographical locations. Seeds were obtained from a slow-growing tree in

Lakes Pocosin near Catfish Lake, Craven County, North Carolina, where the peat was more than 4 ft deep. The other pond pine seed source was a rapidly growing tree on a sand ridge 140 mi. southwest of Catfish Lake in Horry County South Carolina.

Loblolly pine seeds were obtained from a well-formed tree in a swamp in Carteret County, North Carolina.

Figure 1 shows locations of both the seed sources and the sites from which soils were obtained.

FIG. 1. Locations of seed sources and study areas.

RESULTS

LOCATION AND PHYTOSOCIOLOGY OF SAMPLED SITES

The Pinus/Cyrilla community selected is the most northern of the stands of the present study. This stand lies in a Carolina Bay 12 mi. northeast of Burgaw, Pender County, North Carolina, along the east side of the intersection of the Bear Garden Road and the road connecting with the north entrance of the Holly Shelter Wildlife Refuge.

The vegetation is characteristic of the Pinus/Cyrilla/Woodwardia community described in previous work. The largest stems of shrubs of the Cyrilla union are 20 yrs old and 15 to 20 ft tall. According to Woodwell (1956) site quality for pond pine in such high-bush Pinus/Cyrilla communities is high in comparison with other pocosins. Average site index based on measurements of 5 trees is 56 ft. Coile (1952) reports that on good sites with mineral soils pond pine site index may exceed 90 ft and on the poorest sites, those with deep peat underlain by sand, may be as low as 31 ft. Site index of the Pinus/Cyrilla site of the present study is therefore about 25 ft higher than that of the poorest pocosins.

One half mile east of the Cyrilla stand a Carolina Bay supports a representative stand of the Zenobia union. In this study the stand was designated "Zenobia A." The largest trees are between 97 and 105 yrs old and are 50-55 ft tall. Site index for pond pine, averaged for 5 trees, is 39 ft, 17 ft lower than in the Cyrilla stand 0.5 mi. west. The shrub union, made up of the wide variety of species characteristic of the Zenobia union, is between 2 and 4 ft in height and 10 to 14 yrs old.

The second Zenobia site (Zenobia B) is Tussock Bay, a Carolina Bay about 12 mi. east of Elizabethtown, North Carolina, in Bladen County. The stand was burned in 1950 and subsequently the timber was cut. The trees left standing are between 67 and 114 yrs old and between 40 and 75 ft tall. Average site index, based on 6 trees, is 45 ft.

The present shrub union contains scattered individuals of Zenobia among numerous other common pocosin shrubs. However, *Lyonia lucida* is the most abundant of the shrub species and the community will probably be a Pinus/Lyonia community in a few years.

The southernmost pocosin sampled is a representative of the Pinus/Lyonia community in Georgetown County, South Carolina. The stand is one of the many pocosin stands of the "ridge and bay" topography along the East CCC Road, east of Big Kilsock Bay.

The tree union is 70 ft in height and the oldest trees are about 70 yrs of age. The site index for pond pine, based on 2 trees, is 61. The shrub union is a pure stand of *Lyonia lucida* 17 to 20 yrs old and 12 to 18 ft tall.

The two swamps sampled are both in Carolina bays in Georgetown County, South Carolina. Wide areas in these swamps support the characteristic Nyssa-Taxodium/Magnolia/Lyonia community. The localities from which soil samples were taken were somewhat atypical representatives of these associations in that both localities support scattered loblolly pines. Big Kilsock Bay was sampled at a point near the southwestern edge of the swamp where loblolly pine is present in addition to a representation of those species usually found in the Nyssa-Taxodium community. Site index for loblolly, based on 5 trees, is 75. Tupelo Bay was sampled at the western edge of the swamp adjacent to the International Paper Company Canal, where the site index for loblolly is 85, based on 2 trees near the edge of the swamp.

SOILS

Profiles. The soil profiles of the 4 pocosin sites are characteristic of shallow peat profiles throughout the Coastal Plain. The depth of the organic accumulation varies between 10 and 20 in. and all the sites except Tussock Bay are underlain by coarse black humic sand which is dark gray at a depth of 3 to 4 ft below the soil surface. The organic horizon of Tussock Bay is underlain by chocolate brown humic sand to a depth exceeding 4 ft. These soils do not contain a B-horizon and are true A-C soils.

Tupelo Bay contains deep deposits of black muck throughout most of its area. At the sampled site, however, the surface muck is sandy and is under-

lain to a depth of 3 ft by coarse black humic sand similar to that of the pocosins. The surface organic horizon of Big Kilsock Bay at the place sampled is also muck and is underlain at 1.5 to 3 ft by a gray glei horizon.

Basic Soil Data. The content of organic matter, density of the undisturbed soils, pH and total N for each of the soils appear in Table 1 with a summary of the site indices for the pocosin soils. Organic matter was determined by loss on ignition; N by the Kjeldahl method.

TABLE 1. Basic soil data. Loss on ignition values are means of 10 determinations; density, 4 determinations; total N, 2 determinations. Acidities reported as pH are means of 4 determinations of H-ion concentration.

Soil	LOI (% O.D. Wt.)	Bulk Density	Total N (ppm)	pH	Pond Pine Site Index
Pocosin					
Zenobia A	59.8	0.224	6604	4.00	39
Zenobia B	74.1	0.198	3954	3.52	45
Cyrilla	45.3	0.240	6221	3.80	56
Lyonia	88.2	0.147	13838	3.55	61
Swamp					
Tupelo	27.7	0.485	5515	3.89	—
Big Kilsock	34.9	0.400	10054	4.24	—

The swamp mucks of Big Kilsock and Tupelo Bays have the least organic content with 35% and 28% respectively. The sandy pocosin soils of the Zenobia A and Cyrilla stands contain 60% and 45% organic matter respectively, while Zenobia B and Lyonia contain 74% and 88% organic matter respectively. The pocosin soils of this study are therefore true peats, whereas the swamp soils are organic loams or mucks. The bulk densities of undisturbed 3 × 3 in. core samples of the organic surface horizon, based on 4 determinations for each soil, are between 0.147 g/cc for Lyonia and 0.485 g/cc for Tupelo and parallel the loss on ignition values.

Total N is highest in the Lyonia and Big Kilsock soils with approximately 14,000 and 10,000 ppm respectively and lowest in the Zenobia B and Tupelo soils with approximately 4,000 and 5,000 ppm respectively. Zenobia A and Cyrilla contain about 6,000 ppm N each.

Moisture Characteristics. The importance of soil texture and structure in determining soil water relations is outlined by Kramer (1949). Because the texture and structure of organic soils are variable, the water relations of these soils under similar moisture regimes may be quite different. One criterion for evaluating physical characteristics of the soil is the soil moisture characteristics curve. Undisturbed samples were used to determine 5 points on the soil moisture curves of the 6 soils. The porous plate and pressure membrane apparatus were used for the ⅓, 1, 2 and 15 atmosphere moisture contents. An approximation of the field moisture content at saturation was obtained by using samples which had been flooded for one week. The soil moisture curves presented in Figure 2 are expressed in milliliters of

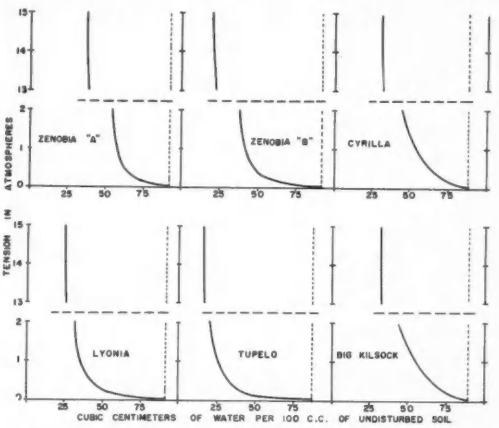

FIG. 2. Soil moisture characteristics curves for the organic horizons of the soils studied.

water retained per 100 cc of soil. Soils were sampled when near field capacity and the soil volume at this moisture content was used in the computations.

The difference between any point on the curves and the approximate saturation moisture content is an estimate of the drained pore space at that moisture tension. A comparison of the drained pore space at ⅓ and 1 atmosphere tensions (Fig. 2) indicates that the 6 soils fall into 2 groups. The Zenobia A, Cyrilla and Big Kilsock soils are less well-aerated with between 23 and 30 cc of drained pore space at ⅓ atmosphere and between 35 and 43 cc at 1 atmosphere. Zenobia B, Lyonia and Tupelo are better aerated with between 45 and 56 cc of drained pore space at ⅓ atmosphere and 50 and 66 cc at 1 atmosphere.

Nutrient Analyses. Analyses of the nutrient elements contained in acid extracts of the soils (Table 2) were made by the North Carolina Department of Agriculture.

TABLE 2. Soil nutrient analyses made by the North Carolina Department of Agriculture. Figures are means of 2 determinations and express concentrations in ppm of oven dry soil.

Soil	Soluble Salts	NO_3	P	K	Ca	Mg
Pocosin						
Zenobia A	<150	1.5	2.80	107.5	100.20	173.9
Zenobia B	<150	1.5	2.50	63.7	25.00	68.1
Cyrilla	<150	1.0	2.16	80.5	90.00	128.9
Lyonia	600	39.0	3.50	46.1	30.06	75.4
Swamps						
Tupelo	600	26.0	6.00	29.9	150.00	36.5
Big Kilsock	600	39.0	4.50	29.3	150.00	8.5
Leached Sand	<150	0.75	3.50	5.9	10.00	0.0

In general the nutrients of these soils are low in comparison with a tilled soil fertile for corn, a crop requiring comparatively low nutrient levels. The swamp and the Lyonia soils contain N, P, and K in concentrations which approximate the fertility range

of a tilled soil. The other soils contain low levels of N and P and comparatively high levels of K. Ca in the swamp soils is higher than in the pocosins, but in all soils is below the range required for the culture of corn. Deficiencies of N, P and Ca might be expected to occur in a crop plant grown in any of the organic soils, but would be most severe in the pocosin soils.

Soil Characteristics and Site Index. The present study was a search for factors causing gross differences in site quality among pocosins. Comparison of site index (Table 1) with the various physical constants determined indicates no obvious correlation. Although each of these constants probably has a direct effect on site quality and may have several indirect effects, these effects are too small to be recognizable in this study.

Similarly, the analyses of the nutrients contained in acid extracts of the soils show no obvious correlation with site quality. N, P and Ca would probably be deficient for a crop plant in all the soils. The nutrient requirements of trees are not well known.

SOIL POT CULTURE TESTS OF PINE AND OAT GROWTH

Design of the Experiment. The objectives of the preliminary experiment were first, to determine whether the differences in site quality among the six soils could be demonstrated in the greenhouse under experimental conditions; second, to discover whether deficiencies of specific nutrients might be important in limiting plant growth in these soils.

A randomized block experiment was designed incorporating tests of the availability of various nutrient elements (after Allard 1942) with tests of plant growth in the 6 soils under greenhouse conditions. The experiment provided for growth tests of oats and of pond pine of Lakes Pocosin origin.

The basic solution used was Hoagland's No. 2 (Bonner & Galston 1952). The nutrient elements N, P, K, S, Ca and Mg combined, and trace and iron combined, were systematically eliminated from this solution to make a total of seven solutions. A distilled water control was the eighth treatment and provided the tests of growth in the untreated soils. A control soil of leached sand provided a check on the nutrient solutions. The acidity of all solutions was adjusted to pH 3.5 with hydrochloric acid. No buffer was used. The experiment was set up in the nutrient bench described under "Methods." Three tanks, each containing 14 pots, provided 3 replications of each treatment.

The nutrient salts were allowed to accumulate in the soils for 2 months when the soil solution contained about 1.5 times the standard concentration of Hoagland's solution.

Tests Using Oats. Twenty-five seeds of oats were planted in each pot and the plants were harvested 43 days after planting by cutting off the stems at the ground level. The mean oven dry weights of oats, averaged for the 3 replications, appear in Table 3.

The response of the oats to nutrient treatment varied significantly among the soils. The soil means, averaged over all treatments, show that the best growth of oats occurred in the swamp soils, both of which produced significantly better yields than either the sand cultures or any of the pocosin soils. The mean yield for the Cyrilla soil cultures was the same as that for the sand cultures while all other pocosin soils produced significantly smaller yields than the sand cultures. Growth of the oats in the water cultures of all the soils was poor and comparisons with the sand control do not show significant differences, indicating that the differences in the soil means for the experiment are due in part to interaction of soils and nutrients. In the Zenobia (A,B) and Lyonia soils this interaction resulted in significantly smaller yields than occurred in the sand cultures and these soils, therefore, inhibited the utilization of the nutrient solution by oats. The inhibition did not occur in the other soils and the experiment gives no indication of the nature of the inhibition.

The inhibition of oat growth was most severe in the Zenobia soil cultures and resulted in yields in all treatments which were below the magnitude of the difference required for significance. Nutrient deficiencies, therefore, could not be diagnosed with confidence in these soils.

However, Table 3 provides estimates of the availability in these soils of each of the nutrient elements N, P, K, S, Ca and Mg combined, and trace and Fe combined, when other elements are supplied in abundance. The effect on the growth of the oats of the removal of each of these elements from the complete nutrient is shown by the sand cultures. In these cultures the removal of any element except trace and Fe resulted in a significant reduction in growth from that in the sand culture supplied the complete nutrient. Therefore, if no complicating interactions occurred, the growth of oats in any soil failing to supply in abundance any nutrient except trace and Fe might also be significantly less than growth in the complete nutrient treatment of that soil.

TABLE 3. Mean oven dry weights of oats in milligrams averaged for three replications. Significant difference within the table is 806 mg; between treatment means is 214 mg; between soil means is 199 mg.

Treatments	Soils							Treatment Means
	Zenobia A	Zenobia B	Cyrilla	Lyonia	Tupelo	Big Kilsock	Sand	
Complete	780⁻	377⁻	2137*	980*⁻	2443*	2010*	2667*	1628*
−N	60	10	23	27	433	1080⁻	57	241
−P	983	207	1133*	293	2633*⁻	1013	767	1052*
−K	1137*	280	1353*	450	2053*⁻	2060*⁻	687	1146*
−S	800	430	1363*	480	2550*⁻	1227	750	1086*
−(Ca+Mg)	536	200	396	250	1580⁻	1197⁻	223	626*
−(Tr+Fe)	390⁻	350⁻	1073*	693⁻	2413*	2553*	2110*	1369*
H_2O	290	37	93	120	1043	580	303	352
Soil means	622⁻	236⁻	947	453⁻	1894⁻	1465⁻	945	

*⁻Indicate significant differences from water and sand controls respectively (5% level).

Using a significant difference between growth in the complete treatment and growth in any other treatment as a criterion, the relative availability for oats of each of the nutrients tested in each of the soils can be summarized. In Table 4 availability or deficiency proved at the 5% level is recorded as "a" or "d" respectively. Where an indication of either occurred at a higher level, the letter is enclosed in brackets.

TABLE 4. Relative availabilities of the nutrient elements to oats in the six soils. Brackets indicate a probable condition not proved at the 5% level; d = deficient; a = available.

Treatments	Soils					
	Zenobia A	Zenobia B	Cyrilla	Lyonia	Tupelo	Big Kilsock
N	(d)	(d)	d	d	d	d
P	(a)		d	d	a	d
K	(a)		d	a	a	a
S	(a)	(a)	d	(a)	a	d
Ca+Mg			d	(d)	d	d
Tr+Fe		(a)	d	(a)	a	a

The nutrient deficiencies commonly limiting the growth of oats in these soils (Table 4) are deficiencies of N, P and Ca or Mg. P is not limiting in soil from Tupelo Bay. All the nutrient elements tested are deficient in the Cyrilla soil, but this soil, unlike the other pocosin soils, does not inhibit the utilization of the nutrient solution.

Tests Using Pond Pine. Pine seeds from Lakes Pocosin were planted on August 10th, and the seedlings were harvested after 134 days on December 23, 1956. In harvesting, soil was carefully washed from the roots and the seedlings were placed in water until they could be examined for mycorrhizae, photographed, dried and weighed. The seedlings were dried in an electric oven at 70°C and weighed to the nearest milligram. Weights, averaged for the three replications, appear in Table 5.

Interpretation of this experiment is complicated by failure of the pine seedlings to survive in sand cultures supplied complete nutrient solution. At the end of the experiment one pine of the 3 replications of this treatment was dead and the surviving 2 seedlings were chlorotic and dying. Seedlings in the sand cultures of the -(trace and Fe) treatment showed similar symptoms, although all seedlings were living when harvested. Previously applied supplements of ferric tartrate and chelated iron had failed to produce recovery.

Inhibition by the nutrient was not manifest in seedlings grown either in organic soils or in the sand cultures supplied any of the other nutrient solutions. Best seedling growth in the sand cultures occurred in the -S treatment, suggesting that the inhibition by the nutrient might be related to the SO_4 anion. The experiment provided no proof of this, however.

Comparison of the soil means of Table 5 indicates

TABLE 5. Mean oven-dry weights of pine seedlings in milligrams averaged for the 3 replications of the preliminary experiment. Significant difference within the table is 257 mg; between the treatment means is 68 mg; between the soil means is 64 mg.

Treatments	Soils							Treatment Means
	Zenobia A	Zenobia B	Cyrilla	Lyonia	Tupelo	Big Kilsock	Sand	
Complete	245	436*	580*	333	285	409	64	336*
−N	245	31	256	188	197	452	121	213
−P	177	272	354	192	162	271	160	227*
−K	320	402*	621*	281	312	416	45	344*
−S	303	553*	643*	401	215	470	352*	420*
−(Ca+Mg)	394*	373*	571*	409	217	353	151	353*
−(Tr+Fe)	284	365*	568*	347	130	336	94	303*
H_2O	90	106	139	181	146	332	72	152
Soil means	257	317	468	292	208	380	132	

*Indicate significant differences from water and sand control respectively.

that the net effect of the organic soils on pine growth was stimulative. Additional comparisons within the table indicate that the tendency toward stimulation is general throughout the experiment and is probably not attributable to an interaction of the soil with any single nutrient element.

The apparent relative availability to pine of the nutrients tested is summarized in Table 6 using the same analytical system and the same notation used for the oats.

TABLE 6. Relative availability of nutrient elements to pine seedlings in the 6 soils tested. Brackets indicate that the condition is probable but has not been proved at the 5% level; d = deficient; a = available.

Treatments	Soils						Treatment Means
	Zenobia A	Zenobia B	Cyrilla	Lyonia	Tupelo	Big Kilsock	
N		d	d	(d)		a	d
P		(d)	d				d
K	a	a	a	a	a	a	a
S	(a)	a	a	(a)	(a)	(a)	a
Ca+Mg	(a)	(a)	a	a	(a)	(a)	a
Tr+Fe	(a)	a	a	a	(a)	(a)	a

Deficiencies of N and P are the principal nutrient deficiencies limiting pine seedling growth in these soils. N was available in the Big Kilsock soil and probably accounts in part for the superior growth of seedlings in that soil. Elements other than N and P are sufficiently available in all soils for vigorous growth of pine seedlings under the conditions of this experiment.

CORRELATION OF PINE SEEDLING GROWTH WITH SITE INDEX

Comparison of seedling weights of pines grown in the water treatment of the pocosin soils (Table 5) with site index (Table 1) indicates a high degree of correlation. The regression (Fig. 3) of these weights on site index is significant at the 5% level, a correla-

tion which supports the hypothesis that the causes of the differences in site index among these pocosins are associated with the organic horizon.

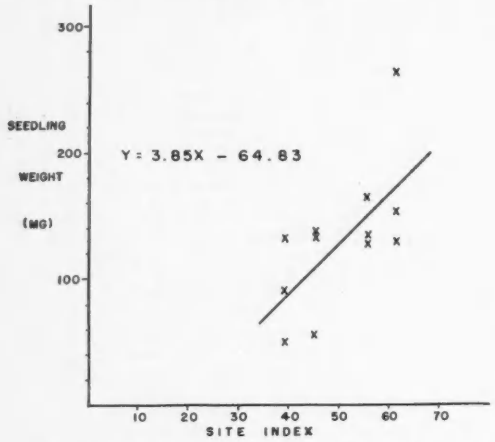

FIG. 3. Regression of seedling weight on site index. Regression accounts for 41% of the variation.

Effect of Mycotrophy on Seedling Growth. Mycotrophy is sometimes of importance in determining the rate of pine growth on relatively infertile sites and may, therefore, be of importance in pocosins. If so, infection, transmitted by the soils, might have an effect on seedling growth. Using the presence of coralloid branching as the only criterion, the presence or absence of infection was noted for each seedling of the experiment. By analysis of covariance the presence of infection was shown to be correlated with an average decrease of 154 mg (±149) in the weight of each seedling infected.

Two interpretations of this negative correlation are possible. First, the mycorrhizae may have caused the decrease in seedling growth; second, the incidence of infection may have been greater on seedlings subjected to poor culture conditions.

Previous studies have shown that the second interpretation is probably correct. The reviews by both Boyce (1948) and Kelley (1950) indicate that mycorrhizae occur most abundantly in poor soils and that the infection is beneficial to the higher plant. In the present experiment the true effect of the mycorrhizae was probably to increase the growth of seedlings grown under unfavorable conditions, thereby reducing the apparent differences in growth between good and poor culture conditions.

Subsequent research took two channels indicated by these experiments. First, the nutrient requirements of the pond pine were investigated; second, an effort was made to determine the causes of the divergent characteristics of the 6 organic soils.

DETERMINING NUTRIENT REQUIREMENTS OF POND AND LOBLOLLY PINES IN SAND CULTURE

Design of the Experiment. The survival of the pond pine under the extreme edaphic conditions of pocosins and the erratic growth of pond pine seedlings in nutrient culture indicated that the mineral nutrient requirements of the pond pine might differ from those of other pines. Therefore, a systematic study of the response of pond pine to various nutrient elements was undertaken after the procedure of Mitchell (1939).

In the previous experiments pond pine seeds from Lakes Pocosin only were used. In the present experiment seeds from Horry County, S.C. and loblolly seeds from Carteret County, N.C. were also included. A randomized block nutrient experiment was planned to provide a comparison of the response of seedlings raised from these three seed lots to variations in nutrients.

A standard nutrient solution for pond pine was devised having generally lower levels of nutrients than the Hoagland's solution used previously. With the new solution as a standard the concentrations of N, P, K, S, Ca and Mg were varied individually at three levels in addition to the level supplied in the standard solution and in addition to zero. The effect of each of the nutrient elements, therefore, was tested at five levels. The concentrations of the nutrient elements supplied by the standard solution appear in Table 7.

TABLE 7. Concentrations of nutrient elements supplied by the standard solution used in study of pond and loblolly pine nutrition. Concentrations expressed in ppm of nutrient solution. Fe and trace were supplied all treatments.

Nutrient Elements	N	P	K	S	Ca	Mg
Parts per million	100	100	100	50	75	50
Salt Source	NH_4NO_3	NaH_2PO_4 KH_2PO_4	KH_2PO_4 KCl	$MgSO_4$ $NaHSO_4$	$CaCl_2$	$MgCl_2$

The experiment was set up in a greenhouse bench according to the system outlined under "Methods." Coarse white sand from near White Lake, N.C. was leached for 24 hrs with 0.1 M HCl and washed with tap water. Each tank in the greenhouse bench contained two plastic pots for each of the seed sources. There were two tanks for each level of each nutrient treatment or 56 tanks in all, containing a total of 336 pots.

Ten seeds per pot were planted on January 16th and seedlings were harvested 120 days later on May 15, 1957. Seedlings were thinned where possible to 4 per pot, one month after planting. Statistical weighting was used to account for differences in the numbers of seedlings in each pot. Harvesting was accomplished by carefully washing out the roots and drying the seedlings at 70°C for 24 hrs. Tops and roots were weighed separately for each pot to the nearest 0.01 gm.

Nutrient solutions were applied in 2 stages. One-half the total concentration was supplied on January

16th at the start of the experiment. This nutrient was allowed to accumulate in the sand until March 25th when the second half of the total concentration was supplied. Within 2 weeks most of this solution had been absorbed by the sand and the jugs were refilled with distilled water. The concentration of nutrient salts in the sand reached its maximum about April 10th. The accumulation of the nutrient salts at the sand surface was reduced by periodically watering the pots from above with a sprinkling can. A total of approximately 3 ppm of iron as ferric tartrate was supplied to all cultures in this manner.

The acidity of the nutrient solutions was set at pH 3.5 on January 16th and again on March 25th using HCl. No buffer was used.

Results. Growth response curves for the 7 treatments are graphed in Figure 4.

In the system of nomenclature for growth curves used by Mitchell (1939) and Gast (1937) that section of the curve over which an increase in the concentration of nutrients produces slight increase in seedling weight is called the "region of the optimum" concentration. Although both Mitchell and Gast defined other regions in the curves, the region of the optimum will be a sufficient reference point for this discussion.

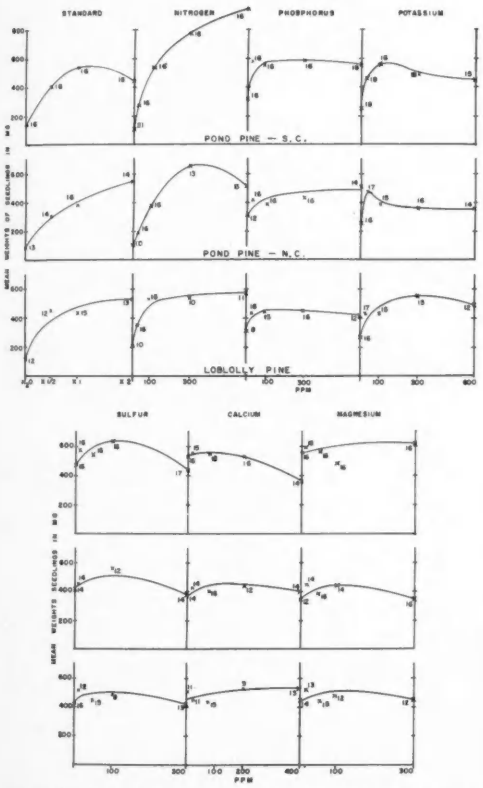

FIG. 4. Growth of pine seedlings in nutrient solutions. Concentrations of standard solution expressed in fractions of normal concentration (×1). Concentrations of elements expressed in ppm of solution. On any curve a difference of 133 mg between points of weight 16 is significant at the 5% level. The probability is 95% that any point of weight 16 lies within 94 mg of the values indicated.

The regions of the optimum, summarized in Table 8 for seedlings of the 3 seed sources, show that considerable variation occurred not only between pond pine and loblolly but also between pond pine seedlings of the two seed sources. The curves of Fig. 4 show that variation occurred in response to differences in the concentration of the standard solution as well as to differences in the concentrations of individual elements. The curves for the standard treatment for instance, show that the growth of pond pine seedlings of Horry County origin was best at the normal concentration of the standard solution. Pond pine seedlings raised from Lakes Pocosin seed and the loblolly seedlings grew best at twice the normal concentration of the standard solution.

TABLE 8. Summary of the concentration ranges through which the best growth of pine seedlings occurred.

Seed Source	N	P	K	S	Ca	Mg
Horry County	300-600+	40-600	45-125	12-100	20-100	25-100
Lakes Pocosin	250-350	40-600+	20-50	12-100	20-100	25-100
Loblolly	75-600	40-600	25-300	12-100	20-400+	25-100

The regions of the optimum (Table 8) indicate that the principal differences between the pond pines occurred in the N and K series. In these series the region of the optimum for the Horry County seedlings was higher, extending for N and K respectively to 600 and 125 ppm. The regions of the optimum for the Lakes Pocosin seedlings in the N and K series lie below 350 and 50 ppm respectively. The regions of the optimum for all other nutrient series are approximately identical for pond pine seedlings of both seed sources.

The regions of the optimum for loblolly seedlings are more broad and slightly higher than for pond pines from either seed source. In the N series the optimum region extended for loblolly between 75 and 600 ppm, the highest concentration of N tested. Similarly the range for K and Ca extended between 25 and 300 ppm and 20 and 400 ppm respectively. In the P, S, and Mg series the optimum region was identical for seedlings of the 3 seed sources. These regions were: P, 40-600 ppm; S, 12-100 ppm; and Mg, 25-100 ppm.

Throughout the experiment pond pine seedlings from the Horry County seed were taller, heavier, and generally more vigorous than seedlings from the Lakes Pocosin seed.

Discussion. The determination of growth response to variations in concentration of a nutrient element is subject to several sources of error. The random errors common to all biological work can be evaluated. More difficult to evaluate are errors introduced as interactions between nutrient elements.

Bear & Toth (1948) showed for example that in certain acid sandy New Jersey soils the uptake of Ca, Mg, and K by alfalfa were closely inter-related. Prianishnikov's (1951) review of nitrogen nutrition in plants indicates that increased concentration of Ca in nutrient cultures is favorable to ammonium absorption and hinders nitrate absorption by plants. Other similar interactions undoubtedly occur and in the present work their effects are confounded with the man effects tested. The results of the present experiment show, therefore, not the direct effect of various concentrations of the elements on plant growth, but the effects of these concentrations when other elements are present in the stated quantities.

Two additional sources of errors could not be evaluated in the present experiment. Neither the total concentrations of Na or Cl ions nor the total concentration of salts in the solutions could be controlled. The specific effects of Na and Cl ions on pond and loblolly pine have never been investigated. However, low concentrations of these ions are usually not harmful to plants and their presence may improve the growth of certain plants (Meyer & Anderson 1952). Mitchell (1934) found that the chloride content of his solutions had no effect on white pine seedling growth.

The osmotic pressure of the nutrient solutions did not exceed ½ atmosphere according to conductivity measurements made using the methods of the U.S. Regional Salinity Laboratory (Richards 1954). It is doubtful that differences in osmotic pressures within this range contributed significantly to the differences in plant growth among the treatments.

The superior growth of the Horry County seedlings may have been due to the greater average size of the Horry County seeds. The tree from which the Horry County seeds were obtained was fast-growing with longer needles, larger cones, and larger seeds than the seed tree of Lakes Pocosin. Gast (1937) and Mitchell (1939) showed that seedling size is correlated with seed weight in short term experiments. Weights of 20 seeds taken at random from each seed lot of the present experiment indicate that the seeds of the Horry County collection are 3.16 mg heavier than the seeds of the Lakes Pocosin collection. The probability is 75% that this difference is real. Although no test of the effects of seed weight was incorporated into this experiment, the greater weight of the Horry County seedlings may be due to the greater weight of the seeds, or to hereditary differences.

Comparison of the regions of the optimum listed in Table 8 with the nutrient levels supplied by the normal concentration of the standard solution shown in Table 7 indicates that the best growth of seedlings from all seed sources would occur in a solution modified to that listed in Table 9 below. These nutrient levels, with nutrients supplied as the salts used in the present experiment, would probably be optimum for the culture of either pond or loblolly pine for at least 6 months.

TABLE 9. The standard solution corrected according to the regions of the optimum of Table 8. All concentrations in ppm.

	N	P	K	S	Ca	Mg
Corrected standard solution...	300	100	50	50	75	50

EFFECT OF ACIDITY ON GROWTH OF OATS IN ORGANIC SOILS

To determine the nature of the inhibitory effect of the soils on the utilization of nutrient solution by oats, extracts of the Zenobia B and Big Kilsock soils were applied to oats growing in leached sand. These soils were selected respectively as representative of those soils in which inhibition did and did not occur in the earlier experiments. Three liters of soil were thoroughly mixed with 6 liters of each of the solutions listed below. Acidity was adjusted using HCl and NaOH.

Solution	*pH*
distilled water	not adjusted
distilled water	3.0
distilled water	6.0
Hoagland's solution	3.0
Hoagland's solution	6.0

After the mixtures had settled for 2 hrs the supernatant liquid was applied to oats growing in coarse leached sand in a nutrient bench similar to that described under "Methods."

Twenty-five seeds of oats were planted in each pot and 3 pots were used per tank. Tanks were not replicated. Oats were harvested after 32 days on May 2nd, oven dried at 70°C and weighed to the nearest 0.01 gm. The mean yields averaged over the three pots of each tank appear in Table 10.

TABLE 10. Mean yields in milligrams of oats raised in leachates of peat. Significant difference within the table is 243 mg; between treatment means is 106.5 mg; between soil means is 80.0 mg.

	Treatments					
Soils	H_2O	H_2O pH 3.0	H_2O pH 6.0	Hoag'd's pH 3.0	Haog'd's pH 6.0	Soil Means
Control	283	243	290	1370*	1412*	721.7
Big Kilsock	463	156*	473	290−	860*−	448.7−
Zenobia B	393	2?2	363	137*˙	597−	356.3−
Treatment Means	383	230.5*	375.5	5?8.9*	956 1*	

*Indicate significant differences from water and sand controls respectively (5% level).

Comparison of the soil means shows that the net effect of the organic soil solutions on the oats over the whole experiment was an inhibition of growth. Among the treatments, the best growth occurred in cultures supplied Hoagland's solution at pH 6.0 and the poorest growth in cultures supplied water at pH 3.0.

A systematic comparison of the yields of oats shown in Table 10 indicates that pH had an effect on growth only when the solutions were mixed with the soils. No significant difference in the yields occurred among the control cultures treated with water at any pH. Neither was there a significant difference between the control cultures treated with Hoagland's solution at pH 3.0 and pH 6.0. Acidity alone, therefore, does not directly affect the yields of oats under these conditions.

On the other hand, among the Big Kilsock Bay cultures, the yields of oats supplied with water at pH 3.0 were significantly smaller than those of either the cultures supplied with H_2O at pH 6.0 or H_2O pH not adjusted. Similarly, Zenobia B H_2O pH 3.0 cultures produced yields which were smaller than the H_2O pH 6.0 or the H_2O cultures of the same soil, but the differences were below significance. The Hoagland's pH 3.0 cultures of both organic soils produced yields which were significantly smaller than the yields of the Hoagland's pH 6.0 cultures.

Poor yields of oats, therefore, are correlated with low pH in the soils and not with low pH in the nutrient solutions. Apparently certain nutrient elements become unavailable in these soils at low pH or some substance inhibitory to oats is released by the soils.

Fixation of Soil Phosphates

Phosphorus deficiency is a common nutrient deficiency in highly acid soils. In such soils phosphates may be present but rendered insoluble, and therefore probably unavailable to plants, by precipitation with iron and aluminum compounds (Russell 1950). Salisbury (1954) showed by consideration of the law of mass action that simple equilibrium conditions prevail between iron and phosphate in the soil solution of acid mineral soils in Utah. Puri (1949) also believes that the removal of phosphates from solution is usually through simple precipitation as insoluble salts. Dean & Rubins (1947), however, demonstrated that phosphates may be bound by an anion exchange system of the soil and under these conditions are replaceable with fluoride.

To determine whether phosphorus was immobilized by the 6 soils approximately 20-gm soil samples were shaken mechanically with 100 ml of water plus various concentrations of KH_2PO_4. The phosphate concentration of the supernatant liquid was determined colorimetrically. No attempt was made to control pH. The pH of the pocosin soil suspensions at the highest concentration of KH_2PO_4 used was 3.0. The pH's of Tupelo and Big Kilsock at the highest concentration were 3.5 and 3.8 respectively.

The curves of Figure 5 indicate that the soils have varying capacities for removing phosphates from solution. Low concentrations of phosphate are not removed by either the Zenobia A, B or the Cyrilla soils. Concentrations up to about 50 ppm are entirely removed by the Lyonia and swamp soils. All soils except Tupelo remove increasing amounts as the concentrations of phosphates in the soil solution increase.

It was demonstrated that small quantities of charcoal remove phosphate anions from solution. Treatment of the charcoal suspension with ammonium fluoride after the method of Bray & Kurtz (1945) resulted in the total replacement of the phosphate by fluoride. Similar treatment of the soil suspensions, however, did not result in the release of phosphate into solution under any conditions, indicating that the phosphate removed by the soils is probably fixed chemically and not adsorbed by an anion exchange mechanism.

Effect of N and P on the Growth of Oats and Pine Seedlings in Organic Soils

Design of the Experiment. Because N and P appeared to be the principal deficiencies in these soils an experiment was designed to test the effects of the application of excess N and P together and separately on both oats and pines growing in the 6 soils. N was supplied as NH_4NO_3 and P as NaH_2PO_4 to plants in plastic pots in the nutrient bench. Four treatments were used: one each in which N and P were supplied separately, one in which equal quantities of N and P were supplied, and one in which distilled water was supplied without nutrients. Each tank was replicated once. Equal numbers of seeds were planted in each pot and the pines were thinned to four seedlings per pot after two months. Lakes Pocosin pine seeds were used. No seedlings died.

To obtain uniform soil texture among the 6 soils, the organic material was thoroughly mixed with coarse, leached white sand in the proportion 4 parts sand to one part organic matter by volume. During the first month sufficient nutrient was supplied to raise the total concentration of nutrient salts to 100 ppm in all cultures. Subsequently this level was raised to more than 500 ppm.

Effect of N and P on Oats. The oats were harvested after 57 days on March 25th. Mean oven dry weights per pot, in milligrams averaged for the 2 replications, appear in Table 11.

None of the treatments applied affected the growth

Table 11. Mean oven-dry weights of oats treated with N and P. Significant difference within the table is 731 mg; between the soil means is 183.1 mg; between the treatment means is 131.8 mg.

Treatments	Soils							Treatment Means
	Zenobia A	Zenobia B	Cyrilla	Lyonia	Tupelo	Big Kilsock	Sand	
N	301	156	307	403	622	618	691	443
P	250	126	189	324	524	631	745	406
N+P	250	188	284	348	579	669	720	433
H_2O	214	126	221	323	524	618	607	378
Soil Means	254⁻	163⁻	251⁻	350⁻	562	634	691	

⁻Indicates significant difference from sand control.

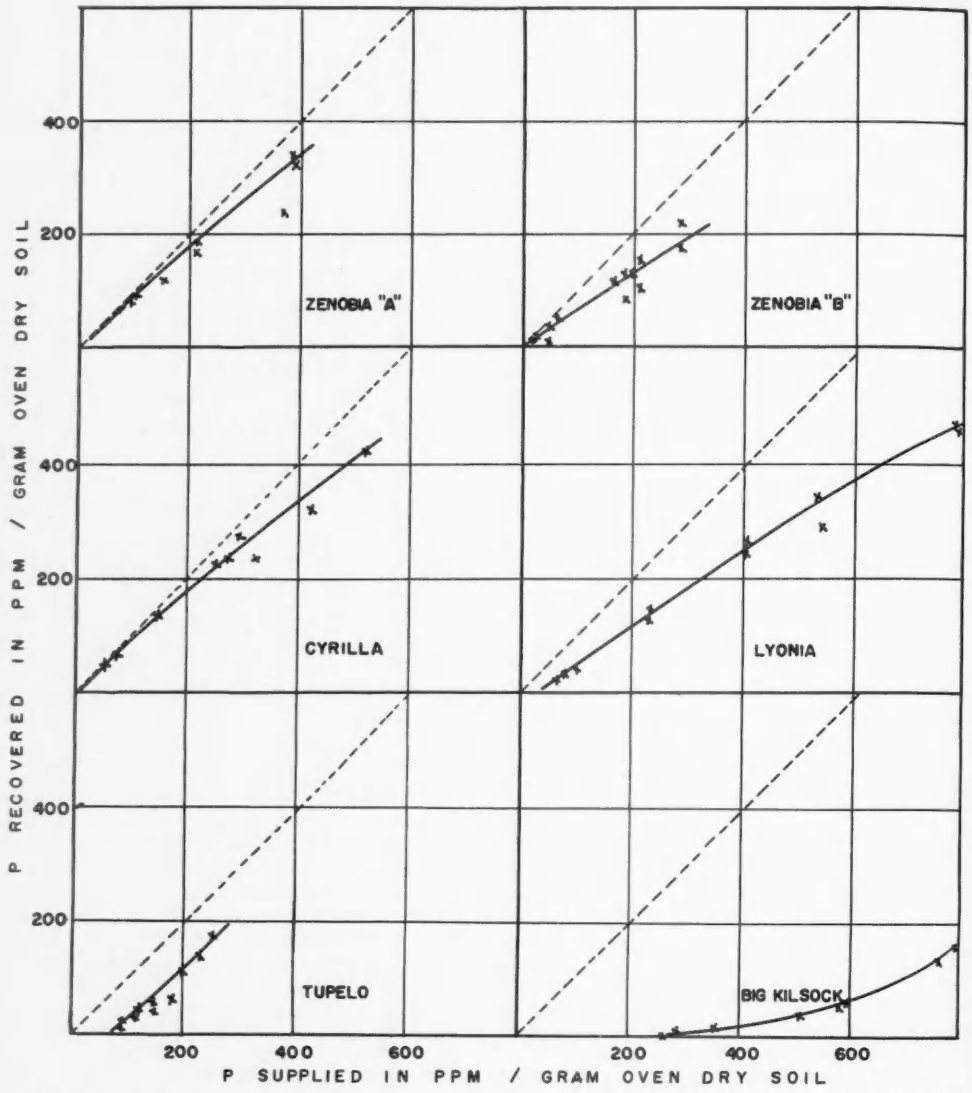

FIG. 5. Soil phosphorus precipitation curves. Dashes indicate phosphorus recovered when no precipitation occurred.

of oats sufficiently for the differences among the treatment means to be significant.

Because the nutrients had no effect on the oats, the extra precision of the soil means can be utilized to examine the relative growth of the oats in the soils. The mean yields for the pocosin soils are significantly lower than the means of the sand cultures or the means of the swamps. The pocosin soils must therefore inhibit the growth of the oats. Because flooding was uniform for all the soils and differences in texture had been minimized, the inhibition cannot be attributed to either of these factors. Neither did deficiencies of the major elements cause the inhibition inasmuch as the leached sand contained generally lower concentrations of these elements than did any of the soils (Table 11).

Effect of N and P on Pine Seedlings. Pine seedlings were harvested after 129 days on June 5th. Soil was washed from the roots and the seedlings from each pot were oven dried and weighed to the nearest 0.01 gm. The mean weights per pot, averaged for the two replications appear in Table 12.

The treatment means indicate that the addition of N, P or N and P together increased the growth of seedlings significantly. However, in each soil these increases were small and those due to N and P alone

TABLE 12. Mean oven-dry weights of pine seedlings treated with N and P. All weights are in milligrams. Significant difference within the table is 337 mg; between treatment means is 118 mg; between soil means is 86 mg.

Treatments	Soils							Treatment Means
	Zenobia A	Zenobia B	Cyrilla	Lyonia	Tupelo	Big Kilsock	Sand	
N	515	600	525	507	460	395	525	512*
P	700	655	550	865⁻	680	550	435	634*
N+P	1685*⁻	960*⁻	1420*⁻	735	930⁻	650	460	971*
H_2O	460	390	510	645	450	475	370	471
Soil Means	672⁻	521⁻	601⁻	562⁻	504⁻	405	358	

*⁻Indicate significant differences from water and sand controls respectively (5% level).

were not significant. The addition of both elements together produced significant increase in growth in all soils except Big Kilsock and Lyonia, although the increase in the Lyonia soil approaches significance. Apparently deficiencies of these elements limit the growth of pond pine in pocosin soils.

Correlation of Seedling Growth with Site Index.

Considerable variation occurred in seedling growth among the soils of the water treatment. Although this variation was not great enough to contain significant differences in any comparison, a regression of seedling weight on site index among the pocosin soils is significant at the 5% level (Fig. 6). This correlation in these cultures in which the organic soils represent only $\frac{1}{5}$ of the total volume of the culture medium indicates that soil texture is probably not the cause of the differences in seedling growth or in site index on these organic soils. The control of soil texture did, however, reduce the variation between the replications from that in the preliminary experiment.

Effect of Mycotrophy on Pine Seedling Growth.

The relative abundance of coralloid mycorrhizae was recorded for the seedlings of each pot on a scale of 0-3. By analysis of covariance the distribution of mycorrhizae was shown to be independent of seedling weight throughout the experiment.

DISCUSSION

USE OF SEEDLINGS TO DETERMINE NUTRIENT REQUIREMENTS OF TREES

The transfer of conclusions based on experiments conducted with tree seedlings to forest stands of commercial potential can be made only with the utmost caution. Lutz & Chandler (1946) cite evidence indicating that nutrient deficiency symptoms in pine may not appear until the trees are 15 to 30 yrs old. In addition the requirements of trees for nutrients varies with changes in other ecological conditions, thereby limiting the scope of any conclusions regarding the optimum nutrient conditions for trees.

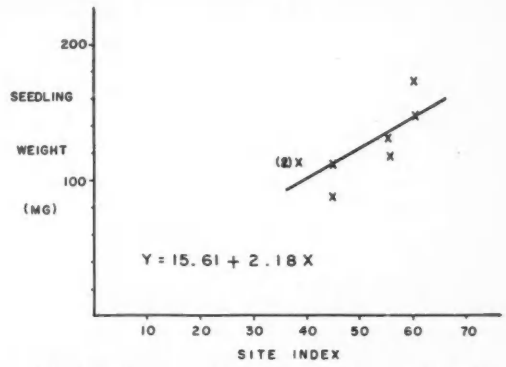

FIG. 6. Regression of seedling weight on site index. Seedlings grown in soils of approximately uniform texture. Regression accounts for 56% of the variation.

In the present study conclusions based on experiments using pine seedlings can be applied reasonably to comparisons with other plants grown under similar conditions and to comparisons of soils. Further extrapolation of these results would probably be unwarranted.

The assumption that correlation of site index with seedling growth proves that the same factors control the growth of trees and seedlings is also unwarranted for two reasons. First, the measurement of site index based on few trees as in the present work is subject to error which may influence the correlation. Second, proof of the correlation can be considered only an indication that in these soils the factors resulting in differences in the heights of trees 50 yrs old also limit the growth of seedlings. Proof that the indication is indeed fact requires first, the identification of the factor or complex of factors which controls seedling growth, second a system for controlling these factors in the field, and third, a number of years to perform the critical experiments with trees. The present study undertook only the first of these procedures.

PLANT NUTRITION IN ORGANIC SOILS

Analyses of acid extracts of the soil solutions of the six organic soils of this study showed the principal deficiencies for a crop plant to be deficiencies of N, P and Ca. Subsequent biological tests of fertility confirmed this and showed that deficiencies of N and P were probably the principal nutrient deficiencies limiting the growth of pond pine seedlings. Pine seedlings grown in pocosin soil pot cultures supplied only N and P together were up to three times heavier than seedlings grown in soil pot cultures treated with water only. The requirement of pond pine seedlings for calcium was shown to be comparatively low in subsequent work, a characteristic which undoubtedly is a competitive advantage to pond pine in the acid low-Ca soils of pocosins.

The nitrogen nutrition of the pond pine is of particular interest in evaluating the nutrition of the tree in peat. Pond pine seedlings raised in the Hoag-

land's solution used in the biological tests of soil nutrient availability were chlorotic. Seedlings grown in the standard nutrient used in the later work were healthy. The principal difference between the two solutions beyond the differences in ion concentrations was the source of N, Hoagland's solution providing most of the N as the nitrate ion and the standard solution supplying N as ammonium nitrate. The hypothesis that the pond pine requires N as the ammonium cation was tested by supplying ammonium chloride to chlorotic seedlings grown in Hoagland's solution. Sixteen seedlings growing in 4 pots were tested in this manner and in all instances the addition of the ammonium chloride cured the chlorosis completely. Apparently pond pine, a tree native to soils in which reducing conditions predominate, requires ammonia nitrogen for proper growth. The soils in the pot cultures of the first experiment performed the reduction of the nitrate or supplied additional ammonia; the sand controls did neither.

Most nitrogen is absorbed by plants as the ammonium or nitrate ions. The sources of these ions in the soils are several but in pocosins the principal sources are probably the decay of organic material and fixed atmospheric nitrogen.

The decay of organic material is generally considered to release nitrogen to the higher plants only when the carbon/nitrogen ratio of the soil is below 10 (Lutz & Chandler 1946), a ratio considered maximum for agricultural soils. Forest soils, however, frequently have C/N ratios exceeding 20. In the present study carbon was determined from loss on ignition, assuming that 58% of the loss on ignition value is carbon (Lutz & Chandler 1946). The lowest ratio, 20, occurred in the Big Kilsock soil; the highest ratio, 110, occurred in the Zenobia B soil. The Tupelo and Lyonia soils had C/N ratios of 29 and 37 respectively; Zenobia A and Cyrilla, 52 and 42. Under these conditions of high C/N ratios most soluble nitrogen is immobilized by soil organisms, a conclusion which is supported by the absence of significant correlation between the ratios and pine seedling growth.

Nitrogen which does become available through decay probably remains in the soil in the form of ammonia, the first product of nitrogen mineralization, for two reasons. First, the oxidation of ammonia to nitrate is thought to be carried out principally by bacteria. Extreme acidity is well-known to inhibit growth of bacteria and the acidity of pocosin soils is very high (Table 1). Second, oxidation of ammonia requires aerobic conditions which probably do not prevail in peats for long periods. Clearly, then, the apparent requirement of pond pine seedlings for ammonia nitrogen is consonant with the soil environment.

Other sources of fixed nitrogen include algae, nodule-forming plants and nitrogen fixed in the atmosphere. Nothing is known concerning the amount of nitrogen fixed by algae on the surface of pocosin soils, although algae are abundant locally. Nodule-forming plants are not known from pocosins. Estimates of the amount of N delivered by rain indicate that 5 to 7 lbs of N per acre are brought annually (Lutz & Chandler 1946). This nitrogen occurs in the atmosphere in organic and mineralized forms and a certain amount of it is unquestionably carried by precipitation to the root zone. The amount of N available to higher plants from this source in any year is probably very small. If an average of 6 lbs of fixed nitrogen per acre is brought from this source and an acre-furrow slice of peat weighs 500,000 lbs (Lyon & Buckman 1950), then the total nitrogen provided would be about 12 ppm, not enough to modify the C/N ratio appreciably. Apparently competition for nitrogen between the higher plants and the organisms of decay is acute and will remain acute as long as the rate of accumulation of carbohydrate in the soil exceeds 10 times the rate of accumulation of nitrogen.

Control of the C/N ratio is possible by direct applications of nitrogen to the soil. Drainage of shallow peats such as the peats of this study would probably be of advantage only to prevent long term flooding, not to accelerate the removal of carbohydrates because deficiencies of N are acute and undoubtedly restrict decay as well as tree growth.

The phosphorus nutrition of pond pine is also of importance in determining site quality in the soils of this study. The phosphorus precipitation curves indicate that phosphates are chemically bound in the Lyonia, Tupelo and Big Kilsock soils. Despite this precipitation of phosphates the Lyonia and Big Kilsock cultures produced vigorous seedlings in the growth tests of nutrient availability. Although growth of seedlings occurs in nutrient culture in the absence of P (Fig. 4), and the requirements of seedlings for best growth under these conditions are comparatively low (40 ppm), it remains difficult to reconcile the superior growth of seedlings in the Big Kilsock cultures of the nutrient test with either the relatively low P level shown by the soil analyses or the phosphate precipitation curves of Figure 4.

Arnon (1953) summarizes the literature on phosphate nutrition indicating that plants are capable of accumulating inorganic phosphorus in the cell sap to concentrations up to several thousand times the concentration in the soil solution. Furthermore he believes that the phosphorus absorbed by plants exists in the soil as water-soluble phosphates and that equilibrium conditions between insoluble soil phosphates and phosphates in the soil solution are attained very rapidly. Salisbury (1954) showed that ponderosa pine is capable of obtaining sufficient phosphate for survival in highly acid Utah soils in which equilibrium conditions exist in the soil solution between soluble and insoluble iron phosphates. Apparently adequate phosphorus nutrition can occur for certain plants when the concentration of phosphate in the soil solution is less than 1 ppm if the soil solution is in equilibrium with some phosphate source. Such a

relationship may explain the growth of pond pine in the low-P soils of pocosins.

If continuous renewal of low concentrations of phosphate in the soil solution is in fact the only requirement for phosphate fertility for pine, then the precipitation of large quantities of phosphorus such as occurs in the Big Kilsock soil may be indicative of favorable plant-phosphorus relations. Conversely, the failure of soils to precipitate phosphates may indicate that the soils contain no reservoir of insoluble phosphate to maintain even that low level of phosphate in the soil solution necessary for good tree growth.

If the soil solution of such an equilibrium system is continuously removed without the addition of phosphate, it is obvious that the phosphate reserves of the soil will be exhausted in time. Installation of uncontrolled drainage may cause this loss in pocosins. The rate at which phosphate leaching would occur would depend on the volume of water percolating through the soil. Pocosins accumulate surface drainage from higher ground and the rate of phosphate leaching may therefore be higher in drained pocosin soils than in upland soils.

Similarly, reserves of K in both peat and sand soils are usually low (Lyon & Buckman 1950) and drainage of pocosins may result in the removal of both the available and the reserve K, thereby initiating a deficiency which does not at present exist for pine seedlings in these soils.

Evidence of Inhibition of Growth

Any study of soil fertility must involve a standard of growth. In the present study of soils known to be low in plant nutrients the standard used was growth which occurred in leached sand supplied with distilled water.

Under this criterion none of the organic soils inhibited growth of the pine seedlings in any treatment, although there was considerable variation in seedling growth among the soils. On the other hand these soils directly inhibited growth of oats in several treatments. In the preliminary experiment the effect of the soils was apparently an interaction with the nutrient solutions which resulted in reduced oat growth in the Lyonia and both Zenobia soils but not in other soils. Subsequently, under conditions in which texture was controlled, inhibition of oats occurred in all the pocosin soils but not in the swamp soils. In still a later experiment inhibition occurred in both the Zenobia B and Big Kilsock soils and was shown to be related indirectly to high acidity.

The cause of the variation in oat growth in successive experiments was not demonstrated. The relationship of the inhibition to pH suggests that aluminum toxicity, well known to affect grasses, may be the cause (Lyon & Buckman 1950).

Pine seedlings are apparently tolerant of the conditions which inhibit oats in these soils. Addition of N and P in excess quantities resulted in substantial increases in seedling growth in the pocosin soils but did not eliminate the differences among them even when the effects of texture were reduced by sand dilutions of the soils. It is possible that variations in pH among the soils might also have an indirect effect on the growth of pine seedlings without producing the gross inhibition characteristic of the oats cultures.

A marked reduction in apparent soil quality for pine seedlings occurred in the Big Kilsock soil of the N-P experiment. The weights of pine seedlings grown in this experiment in the Big Kilsock cultures were the same as the weights of seedlings grown in the sand cultures. No combination of N or P changed this relationship. Apparently the soil characteristics which caused the superior quality of the Big Kilsock soil in the preliminary experiment had been altered either by the sand dilution used in the N-P experiment, or by some chemical change in the soil. Whatever change occurred did not occur in the other soils of the study. Possibly the 6 months' storage period prior to the use of the soil in the N-P experiment resulted in a substantial modification of the soil chemistry. If so, the nature of the change may be of immediate practical importance in the recently drained virgin soil of Big Kilsock Bay, where the rate of oxidation of the surface soil can reasonably be expected to increase sharply.

The nature of any change in soil chemistry which may have occurred is open to conjecture. Apparently the low fertility was not a deficiency of either N, P or N+P. Rather it may have been either a new deficiency of some nutrient element, possibly induced by an increase in the activity of the microflora during storage, or the accumulation of an inhibitory quantity of some substance. The sensitivity of oats to the indirect effects of low pH in the Big Kilsock soil and the relatively short time required for the change in fertility to occur suggest that the change may have been a simple modification of the quantities or types of organic anions present in the soil solution. Struthers & Sieling (1950) demonstrated that iron and aluminum form stable compounds at low pH with organic anions such as malate. Presumably a sudden change in the complement of organic anions present might release aluminum or iron in inhibitory concentrations, although the effects of these ions on pond pine have never been demonstrated.

Evidence of Physiological Variation in Pond Pine

Several studies in recent years have demonstrated the ecological importance of physiological variation among plants (Turesson 1922; Clausen, Keck & Hiesey 1940; Kruckeberg 1954). Most of these studies have dealt primarily with herbs. The occurrence of similar variation within species of trees is more difficult to demonstrate, although the existence of geographical races of trees has long been known (Wakeley 1954; U.S.D.A. 1948). Studies of physiological variation in trees have been generally restricted to observations of growth under similar environmental conditions such as those observations re-

ported by Wright & Baldwin (1957). More specific studies must be made on a short term basis and perforce must deal with seedlings. Conclusions from such studies are to be applied to forest stands with great caution.

In the present study the response of seedlings raised from seeds from two geographical and topographical extremes were compared. The seed trees represented also extremes of vigor, the one being markedly dwarfed, the other tall, rapidly growing and well-formed. The objective of the consideration of seed source was to discover whether variation in the growth of pond pine seedlings from two sources might occur under experimental conditions. No attempt was made to determine the effect of either geographic location, topography or seed weight on seedling growth and these factors were left confounded with seed source. Therefore, although seedlings from the southern seed source were heavier throughout the experiments and the difference was correlated with a difference in seed weight, the cause of the increased growth cannot be specifically assigned.

Seedlings from the two seed sources varied significantly in their responses to nutrient culture. This was particularly apparent not only in the N and K series but also in the Ca series where the growth of seedlings from the southern seed source treated with 400 ppm Ca was reduced significantly below the growth which occurred when Ca was omitted from the nutrient solution. No such sensitivity to Ca appeared among seedlings from the northern seed source.

Prianishnikov's (1951) review of nitrogen nutrition in plants indicates that increasing concentrations of K and Ca ions in nutrient cultures favor increased NO_3 and NH_4 absorption respectively. Apparently the response of seedlings from the two sources to both K and Ca differs and this may be indicative of differences in the nitrogen metabolism between the two populations of trees which the seeds sources represent.

The concentrations of Ca in soils of the Coastal Plain may vary from near zero to well over 1000 ppm in certain fertilized tilled soils. Undisturbed soils may have levels exceeding 400 ppm according to Welch & Nelson (1951). Apparently there is wide variation among virgin soils in available calcium, possibly enough that the distribution of seedlings from the southern source might be affected by their own sensitivity to high concentrations of Ca. The degree to which this is in fact true is most certainly a subject for future research.

SUMMARY AND CONCLUSIONS

1. Increasing land and timber values in recent years have stimulated interest in improving the timber yields of the extensive low-quality wetlands of the Southeast called "pocosins." Drainage has not always resulted in improved tree growth and descriptive studies have indicated that on certain of these sites soil characteristics might be more important than flooding in determining site quality for pond pine, the principal commercial tree. The present study was designed to discover the factors which control the growth of pond pine in pocosin soils.

2. Four pocosin soils from sites representative of 3 vegetation types recognized in earlier work were selected for study. Sites are subject to apparently similar flooding regimes and soil profiles are characteristic of shallow peat profiles of the Coastal Plain. Two of the sites support Pinus/Zenobia communities which are representative of "low-bush" pocosins; one of the sites supports a Pinus/Cyrilla community, the other, a Pinus/Lyonia community. These latter communities are representative of "high-bush" pocosins. Two swamp soils were included to provide a comparison between the theoretically sterile bog peats of the pocosins and the more fertile swamp mucks. Samples of the surface peat were used in all experimental work.

3. In the present study it was thought that soil fertility for pine might be directly related either to differences in the flooding regimes of the surface soils or to differences in soil aeration at low moisture tensions. An estimate of soil aeration was obtained using pore space determined from the soil moisture characteristics curves. No relationship to site quality was apparent. Subsequently pine seedling growth in pot cultures under uniform conditions of flooding and with the influence of soil texture reduced by massive dilutions of the soil with sand was correlated with site index. This correlation under these conditions indicates that site index in pocosins is not always directly related either to flooding or to soil aeration. In addition it indicates that the causes of the differences in site quality in these pocosins are probably chemical characteristics of the surface soil and independent of the soil profile.

4. Analyses of extracts of the soil solution indicated that the N, P and Ca levels in all the soils except the swamps were low for a crop plant. Soil pot culture tests using oats and pond pine seedlings confirmed these deficiencies and indicated that deficiencies of N and P probably were the principal deficiencies limiting pond pine growth. Subsequently pond pine seedlings grown in pocosin soil pot cultures supplied excess of both N and P were up to 3 times heavier than seedlings grown in the water-treated control cultures. These results indicate that deficiencies of both N and P are important in limiting the growth of pond pine in pocosins.

5. Investigation of the nutrient requirements of pond and loblolly pine seedlings in sand culture showed that both species would grow well for at least six months in coarse leached sand when watered from below with a solution designed to increase gradually the concentrations of nutrient elements in the pots to the following levels: N, 300 ppm; P, 100 ppm; K, 50 ppm; S, 50 ppm; Ca, 75 ppm; Mg, 50 ppm. These concentrations are generally lower than the optimum levels for white pine. The nutrient requirements for best growth of pond pine were generally lower than those of loblolly.

6. Pond pine seedlings in nutrient culture re-

quire at least part of their nitrogen supplied as the ammonium cation. Seedlings grown with nitrate as a principal source were chlorotic. Nitrogen in pocosins is probably available primarily as the ammonium cation and the pond pine is therefore well adapted to pocosin soil.

7. The concentration of phosphate in the soil solution of even the best soils for pond pine in this study is probably seldom over a few parts per million and usually less than one part per million. There is evidence indicating that certain plants are capable of obtaining sufficient phosphate under these conditions if the phosphate of the soil solution is in equilibrium with an insoluble phosphate source. Phosphate precipitation curves for the soils studied indicate that such equilibrium conditions may exist in certain pocosin soils. If these equilibrium conditions are important in the nutrition of pond pine, drainage of these soils would result in the removal of any phosphorus reserves present and might ultimately produce severe phosphorus deficiencies.

8. The change in fertility of one of the swamp soils during the study emphasizes the importance of chemical soil characteristics not considered in this work. It is possible that changes in the types and amounts of organic anions in the soil solution result in drastic modifications in the availability of both major and minor elements and thereby exert an important control over plant growth.

9. Pond pine seedlings grown from seeds from two sources varied significantly in their response to nutrient culture. Variation was most prominent in the cultures treated with calcium, where the growth of seedlings from the southern source was inhibited by 400 ppm Ca, the highest concentration used. Optimum requirements for both N and K are different for seedlings from the two seed sources, indicating that physiological variation exists within the species. Soil calcium levels in certain Coastal Plain soils exceed 400 ppm and may restrict site quality for certain populations of pond pine.

10. From this work it is apparent that soil nitrogen and phosphorus together are the principal factors controlling pine seedling growth in the pocosin soils studied. Physiological variation occurs within the pond pine taxon and may influence apparent site quality.

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RESPONSES OF CRESTED WHEATGRASS TO VARIOUS CLIPPING TREATMENTS

C. Wayne Cook, L. A. Stoddart
and Floyd E. Kinsinger[1]

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INTRODUCTION

Range management is a science dealing with the utilization of forage plants by livestock. Unfortunately, responses of a plant to grazing at various seasons of the year, at various frequencies and intensities, and under various environmental conditions are so complex that a set of exact grazing principles cannot be developed, even for a single species. However, since basic principles are seemingly so fundamental to range management, a study was begun in 1946 to accumulate basic data dealing with the responses of crested wheatgrass to grazing.

The primary consideration in the utilization of ranges is continued production of palatable and nutritious forage throughout each grazing season. Certain fundamental principles of plant physiology must be recognized and applied to insure proper utilization of vegetation. Limited knowledge of the exact effects of herbage removal on the physiological responses of plants has hindered scientific management of the range.

Root growth is closely related to forage growth. Therefore, a complete understanding of the physiological responses of plants to forage removal must consider the relation of the underground development to herbage production.

The quality of herbage is of great practical and economic significance since livestock production is not only a reflection of herbage yield but also a reflection of nutrient content. Too often management of ranges has been based upon maximum yield of herbage rather than upon maximum yield of nutrients and livestock.

Because of the importance and wide use of standard crested wheatgrass (*Agropyron desertorum* [Fisch.] Schult.)[2] in developing spring ranges in the

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Contribution of Utah Agricultural Experiment Station, Logan. Publication approved by the director.

[2] Formerly referred to as crested wheatgrass (*Agropyron cristatum*). Material used in this study most nearly fits *Agropyron desertorum* as described by Sarkar (1956). It is a standard crested wheatgrass strain, Utah 42-1.

West, this species was selected for study. The investigations were designed to determine its response to various intensities, frequencies, and seasons of herbage removal under favorable (artificially watered) and unfavorable (arid) environment. The responses were evaluated on the basis of forage yield, chemical composition of herbage, apparent vigor, seed production, root yield, and root reserves.

REVIEW OR LITERATURE

The effect of frequency and intensity of clipping on the yield and vigor of various pasture and range plants has received considerable study. These investigations have dealt with a great variety of conditions and methods and in general they show that yield and vigor decrease as frequency or intensity of clipping is increased (Albertson *et al.* 1953, Aldous 1930a, Baker *et al.* 1947, Blaisdell & Pechanec 1949, Brown 1943, Buckner & Brown 1945, Canfield 1939, Crozier 1897, Ellett & Carrier 1915, Gernert 1936, Graber, *et al.* 1927, Graber & Ream 1931, Holscher 1945, Kennedy 1950, Lang & Barnes 1942, Mott 1944, Newell & Keim 1947, Sampson 1914, Sarvis 1923, Schoffield 1944, Stoddart 1946, Thaine & Heinrichs 1951, Weaver & Hougen 1939, Weinmann 1943 and 1949, Whitman & Helgeson 1946).

Under favorable growing conditions more frequent harvesting at moderate heights sometimes produces greater herbage yield than a single clipping at the end of the growing season (Ahlgren 1938, Goodwin 1940, Lang & Barnes 1942).

Results from many studies dealing with chemical analysis of plant material show that nutritive value of forage decreases with advancing stage of maturity (Baker *et al.* 1947, Bird 1943, Brown 1943, Grandfield 1930, McCarty 1932, Stapledon 1924, Stoddart 1946, and Waters 1915). Therefore, frequent clipping to prevent plants from becoming over mature increases nutritive value at the expense of yield (Aldous 1930a, Carter & Law 1948, Ellett & Carrier 1915, Kennedy 1950, Kennedy & Russell 1948, Newell & Keim 1947, Weinmann 1943 and 1949, Whitman & Helgeson 1946).

Frequent and intense clipping of grasses have both been found to reduce the number of heads and the number of viable seed per head (Blaisdell & Pechanec 1949, Canfield 1939, Hanson & Stoddart 1940, Sampson 1914, Whitman & Helgeson 1946).

Increased frequency and increased intensity of clipping have resulted in decreased yield, depth, and spread of roots (Albertson *et al.* 1953, Biswell & Weaver 1933, Carter & Law 1948, Graber 1931, Hanson & Stoddart 1940, Harrison 1931, Kennedy & Russell 1948).

Many studies have dealt with the effect of clipping on the stored food reserves in the roots. Reserves generally are reduced by frequent and close clipping compared to a single clipping and less close clipping (Aldous 1930b, Brown 1943, Bukey & Weaver 1939, Hanson & Stoddart 1940, McCarty 1932, McCarty & Price 1942, Weinmann 1943, 1948, 1949).

In addition to intensity and frequency of clipping, season of clipping influenced the vigor of the plants and the production of herbage and roots (Aldous 1935, Brown 1943, Bailey & Mayton 1931, McCarty & Price 1942, Stoddart 1946). In general, clipping in the early season was most harmful but in some cases clipping at the time of seed formation was most detrimental.

McCarty & Price (1942) found that plants clipped at advanced stages of maturity had less root reserve than plants clipped earlier and then allowed to grow to maturity.

Several studies have shown that frequent and intense clipping during the growing season almost completely exhausted the carbohydrate reserves of the roots (Hildebrand & Harrison 1939, Kinsinger 1953, Weinmann 1943). Others indicate that nitrogen, phosphorus, and potassium contents of the roots increase with periodic defoliation during the growing season (McIlvanie 1942, Sullivan & Sprague 1943, 1953, Weinmann 1943, 1948b). However, Bukey & Weaver (1939) found no change in mineral content of roots as a result of clipping.

METHOD AND PROCEDURE

This experiment was conducted near Logan in northern Utah on previously dry-farmed wheat land fairly typical of that available for seeding to grass throughout the state. Precipitation averages about 17 in. annually but summers are hot and arid.

Seedlings of crested wheatgrass grown in individual containers in the greenhouse were transplanted to the area in the spring of 1946 and spaced at 3-ft intervals in 4 separate plots consisting of 45 rows each. In each row in each plot there were 22 plants (Fig. 1). Each row was divided into 4 subsamples of 5 plants each with an unused border plant on each end. All plants in rows 1 and 45 were border plants

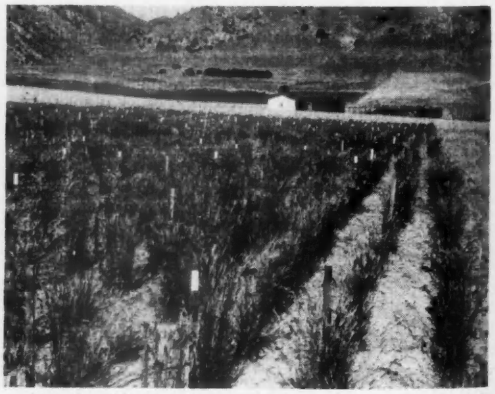

FIG. 1. Plants of crested wheatgrass spaced at 3-ft intervals in rows consisting of 5 plants between colored stakes. The various colors on the stakes designate the treatment.

TABLE 1. Clipping schedule, showing frequency and date of harvesting. (The symbol X indicates a harvesting at the date shown. All plots also were clipped in fall after growth ceased.)

Treatment	Date Clipped										
	April 15		May 1		May 15		June 1		June 15		July 1
1	X	X	X	X	X	X	X	X	X	X	X
2	X		X		X		X		X		X
3	X					X					X
4*											X
5*	X	X	X	X	X	X	X	X	X		
6*	X		X		X		X		X		
7*	X				X				X		
8*									X		
9	X	X	X	X	X	X	X				
10	X		X		X		X				
11	X			X			X				
12*							X				
13	X	X	X	X	X						
14	X		X		X						
15*					X						
16	X	X	X								
17	X		X								
18*			X								
19*	X										
20			X	X	X	X	X	X	X	X	X
21			X		X		X		X		X
22			X				X				X
23					X	X	X	X	X	X	X
24*					X		X		X		X
25					X			X			X
26							X	X	X	X	X
27							X		X		X
28									X	X	X
29									X		X
30			X	X	X	X	X	X	X		
31*			X		X		X		X		
32			X			X			X		
33			X	X	X	X	X				
34			X		X		X				
35					X	X	X	X	X		
36*					X		X		X		
37			X	X	X						
38			X		X						
39					X	X	X				
40					X		X				
41							X	X	X		
42*							X		X		
43*	Unclipped check										

*Chemical analyses of forage were run on these treatments.

Each subsample was permanently marked by a metal tag.

There were 43 harvesting treatments (Table 1) representing various frequencies and seasons. Each of the 43 clipping treatments was superimposed upon 2 different clipping heights. One series of 43 treatments was harvested at 1-in. and a second series of 43 treatments harvested at 3-in. stubble height. All treatments and clipping heights were completely randomized in each plot with 2 subsamples for each in 2 replications. In most cases, the 2 subsamples were composited for statistical analyses.

Herbage from each plant was cut at the end of the second growing season (fall 1948) to eliminate old growth. Differential clipping treatments were commenced the following spring and continued for 5 yrs. Herbage from the 5 plants constituting each subsample was composited and weighed to determine yield. Large butcher knives (Fig. 2) were used to harvest the plants at the desired heights. Clipping forage by hand at a specific height does not exactly duplicate grazing, but it is a practical means of studying responses to herbage removal.

FIG. 2. Harvesting individual crested wheatgrass plants at various heights with large butcher knives. Forage was placed in metal buckets and weighed immediately after collection. Cloth sacks around the bottom of the buckets were to prevent dirt from clinging to the containers.

Two of the plots were watered with overhead sprays and the remaining two received only natural precipitation. Available moisture for the watered and unwatered plots at various depths is shown in Table 2. Late in the summer it was impossible to keep available moisture in the upper layers of soil unless daily applications were made. Since this was not feasible, the plots were watered every 4 days commencing on July 1. Each watering furnished approximately 0.62 in. of moisture. However, this was not considered as effective as an equal amount of natural rainfall because of low humidity and high temperatures. During the peak growing season, March through June, application of water was made on the watered plots as frequently as necessary to maintain available moisture to a depth of 66 in.

In each of the 4 plots, 2 moisture measuring locations were established. Moisture readings were made by means of standardized Bouyoucos blocks (Table 2). Conduction readings were made each week immediately before and again 36 hrs. after each watering. Available moisture was calculated by subtracting the percent moisture at permanent wilting point from the total amount. Permanent

TABLE 2. Average percent available soil moisture at various depths in crested wheatgrass plots for 5 yrs, 1949 to 1953.* Application commenced in June and extended through August.

Moisture condition	Date	6″	12″	18″	30″	42″	66″	Avg.
Watered.....	March	12.8	10.3	13.5	12.5	12.3	11.1	12.1
Unwatered		12.2	11.8	14.0	13.5	11.0	12.4	12.5
Watered.....	April	10.5	13.2	13.1	12.6	12.0	10.0	11.9
Unwatered		10.2	12.7	13.2	13.6	11.6	10.7	12.0
Watered.....	May	9.4	12.8	13.4	13.1	12.3	10.0	11.8
Unwatered		6.9	12.8	13.5	14.6	12.1	10.8	11.8
Watered.....	June	4.5	10.5	12.6	13.8	12.6	11.3	10.9
Unwatered		0.1	4.1	10.6	13.5	12.5	11.1	8.7
Watered.....	July	3.0	7.3	10.1	12.1	11.2	10.6	9.1
Unwatered		0.0	0.0	5.5	9.3	10.1	10.1	5.8
Watered†....	August	0.0	0.0	6.8	9.2	9.7	9.3	5.8
Unwatered		0.0	0.0	0.7	5.3	8.0	7.4	3.6
Watered†....	September	0.0	0.0	1.8	7.1	7.8	8.7	4.2
Unwatered		0.0	0.0	0.0	1.5	5.8	6.1	2.2
Watered†....	October	0.0	0.0	0.0	6.8	8.7	10.7	4.4
Unwatered		0.0	0.0	0.0	3.1	5.6	6.2	2.5

*Available moisture was calculated by subtracting the permanent wilting percentage from the total percentage of water present.

†Moisture readings were made immediately before and 36 hrs. after the application of water at 4-day intervals. Some of the moisture no doubt reached the 6-in. depth shortly after watering but was not present 36 hrs. afterwards late in the season.

wilting points for each depth were determined by the pressure membrane technique at approximately 15 atmospheres tension.

Herbage from 15 selected treatments (Table 1) was chemically analyzed for nitrogen, ether extract, total ash, calcium, phosphorus, lignin, cellulose, and other carbohydrates.

Average number of spikes per plant, filled caryopses per spike, and percent germination were determined for each of the 15 treatments chosen for chemical analysis. These determinations were made at the end of the first season after treatments were initiated, again after 5 yrs. of treatment, and again 1 yr after treatments has ceased.

At the end of the growing season of 1950, 1952, and 1953 plant height and vigor were recorded for all treatments.

During the falls of 1953 and 1954 after 5 and 6 yrs of treatment, root samples were removed from the 15 selected treatments and, in addition, from treatment 10. One complete replication of roots was removed in 1953 and another in 1954. These roots were collected from 3 depths and from 2 plants in each subsample of 5 plants by excavating a column of soil 12 in. square and 18 in. deep (Fig. 3). This column was divided into 0-6, 6-12, and 12-18 in. segments. The 0-6 in. depth included the crowns of the plants. Each collection was washed and weighed separately. Roots were placed in alcohol immediately after they were washed free of soil to prevent enzyme action. Tests showed that no measurable leaching of chemicals occurred during washing. The roots were then chemically analyzed for nitrogen, ether extract, calcium, phosphorus, total ash, lignin, cellulose, and other carbohydrates, hemicellulose, reducing sugars, sucrose, and fructosan.

FIG. 3. Root samples were obtained by excavating around a column of soil 1-ft square and 18 in. deep. This column was divided into 3 segments 0-6, 6-12, and 12-18 in. Each was placed in a box with mesh wire bottom to facilitate washing the soil from the roots.

Roots were excavated in random order so that effect of maturity subsequent to clipping was randomly distributed among treatments and subsamples.

A trench was dug next to each treatment included in the above root study to determine maximum root penetration and area of concentration. Root systems of three plants from each treatment were exposed by removing the soil with an ice pick. A 1 in. layer of soil was removed along with the vertical face of the bisect to the maximum depth of root penetration. Roots emerging from the crown in this 1 in. section were counted. In addition, axial length of each root was measured.

RESULTS

FORAGE YIELD

Herbage production for each treatment was calculated on an air-dry basis in grams per plot, which included 10 plants (Table 3). Production data include herbage removed from all plants in the fall of each year as well as spring yields.

Average yields by treatment for each year are shown in Table 4. All yields decreased from the base year (1948) during the 5 yrs of treatment. The regression coefficients for yield during this period are given in Table 4. The more severe the treatment the larger the annual reduction in forage as shown by the size of the regression coefficients.

Statistical analyses of herbage yield data (Table 5) show annual differences to be highly significant.

EFFECT OF WATER

The overall effect of added water upon production was not significant by an analysis of variance. The basic reason for this lies in the experimental design

TABLE 3. Average air-dry herbage produced per year per plot (10 plants) for 5 yrs for each of 43 treatments clipped at 1- and 3-in. heights on watered and unwatered plots.

Treatment number	Clipping interval	Clipping date*	Clipping frequency	Clipping height	Yield unwatered	Yield watered	Average yield	Lower significant limit†
			times	*inches*	*grams*	*grams*	*grams*	
43	——	——	——	1	3535.5	3133.8	3066.2	2839.8
				3	2912.4	2693.2		
19	——	April 15	1	1	2821.0	2059.1	2546.8	2321.0
				3	2933.4	2373.5		
18	——	May 1	1	1	2012.9	2096.6	2180.1	1956.2
				3	2214.8	2396.1		
15	——	May 15	1	1	1836.2	2059.1	2042.7	1820.1
				3	2169.4	2105.9		
12	——	June 1	1	1	2123.5	2083.8	2061.2	1838.0
				3	1960.0	2077.3		
8	——	June 15	1	1	2413.1	2343.5	2257.8	2032.7
				3	2046.5	2228.0		
4	——	July 1	1	1	2541.3	2990.9	2683.2	2457.4
				3	2460.4	2740.1		
1	One week	April 15 to July 1	11	1	323.6	534.0	564.2	——
				3	543.7	855.3		
5	One week	April 15 to June 15	9	1	327.2	562.9	650.8	475.6
				3	705.3	1007.8		
9	One week	April 15 to June 1	7	1	562.5	1077.4	895.5	700.1
				3	855.0	1086.9		
13	One week	April 15 to May 15	5	1	1165.9	1293.0	1467.9	1247.8
				3	1686.8	1725.8		
16	One week	April 15 to May 1	3	1	1858.3	2070.5	2080.0	1856.1
				3	2112.0	2279.0		
20	One week	May 1 to July 1	9	1	476.3	776.6	731.2	546.5
				3	674.0	997.9		
23	One week	May 15 to July 1	7	1	730.3	1220.8	1057.9	851.7
				3	1053.5	1226.9		
26	One week	June 1 to July 1	5	1	1474.3	1824.2	1680.4	1459.7
				3	1542.7	1880.4		
28	One week	June 15 to July 1	3	1	2442.9	2212.9	2315.1	2090.0
				3	2169.7	2434.8		
30	One week	May 1 to June 15	7	1	722.5	881.6	961.6	762.4
				3	955.5	1286.6		
33	One week	May 1 to June 1	5	1	952.8	1234.3	1243.6	1032.4
				3	1090.8	1696.4		
35	One week	May 15 to June 15	5	1	1435.4	1750.9	1472.0	1251.9
				3	1309.4	1392.4		
37	One week	May 1 to May 15	3	1	1585.4	2020.1	1768.7	1546.7
				3	1562.3	1906.9		
39	One week	May 15 to June 1	3	1	1712.2	2065.6	1748.1	1526.1
				3	1521.5	1693.0		
41	One week	June 1 to June 15	3	1	2169.2	2350.9	2176.7	1952.8
				3	2022.6	2163.9		
2	Two weeks	April 15 to July 1	6	1	601.0	1080.3	881.9	690.8
				3	901.5	944.7		
6	Two weeks	April 15 to June 15	5	1	676.2	1170.6	1007.2	802.9
				3	907.3	1274.8		
10	Two weeks	April 15 to June 1	4	1	883.4	1321.2	1159.6	951.5
				3	987.8	1445.8		
14	Two weeks	April 15 to May 15	3	1	1244.9	1405.3	1451.3	1231.2
				3	1595.0	1560.0		
17	Two weeks	April 15 to May 1	2	1	2087.4	2017.4	2228.3	2003.8
				3	2448.8	2359.4		
21	Two weeks	May 1 to July 1	5	1	710.7	1173.0	975.2	773.5
				3	760.2	1257.0		
24	Two weeks	May 15 to July 1	4	1	1028.0	1450.9	1256.4	1043.9
				3	1240.6	1306.1		
27	Two weeks	June 1 to July 1	3	1	1444.1	2089.9	1715.1	1493.8
				3	1516.8	1809.4		
29	Two weeks	June 15 to July 1	2	1	2264.8	2276.0	2187.7	1963.2
				3	1839.1	2380.8		
31	Two weeks	May 1 to June 15	4	1	1033.4	1310.2	1200.9	990.9
				3	1157.8	1302.2		
34	Two weeks	May 1 to June 1	3	1	1081.2	1413.8	1296.7	1079.2
				3	1153.2	1538.7		
36	Two weeks	May 15 to June 15	3	1	1673.4	1771.1	1602.7	1382.0
				3	1439.7	1526.6		
38	Two weeks	May 1 to May 15	2	1	1522.1	1784.3	1731.2	1509.9
				3	1770.7	1847.5		
40	Two weeks	May 15 to June 1	2	1	1800.1	2227.3	1835.0	1613.0

Table 3 (cont.)

Treatment number	Clipping interval	Clipping date*	Clipping frequency	Clipping height	Yield unwatered	Yield watered	Average yield	Lower significant limit†
				3	1711.1	1601.3		
42	Two weeks	June 1 to June 15	2	1	1928.6	2298.6	2007.9	1785.3
				3	1753.0	2051.2		
11	Three weeks	April 15 to June 1	3	1	1167.0	1348.0	1292.4	1076.1
				3	1217.7	1436.7		
25	Three weeks	May 15 to July 1	3	1	1096.0	1412.2	1287.1	1072.1
				3	1160.7	1479.6		
32	Three weeks	May 1 to June 15	3	1	1032.6	1533.1	1267.0	1053.2
				3	1133.9	1368.4		
7	Four weeks	April 15 to June 15	3	1	1334.1	1513.5	1401.6	1182.2
				3	1243.5	1515.2		
22	Four weeks	May 1 to July 1	3	1	1084.3	1428.7	1301.7	1082.9
				3	1304.8	1389.1		
3	Five weeks	April 15 to July 1	3	1	1045.6	1447.3	1288.5	1072.9
				3	1237.0	1424.2		
				1	1441.0	1677.1	1559.0	
Average				3	1511.2	1698.8	1605.0	
				Average	1476.1	1687.9	1582.0	

*All plants were also clipped once during October and weight of this herbage is included in this table to give total annual production for the treatment.
†Lower significant limit (L.S.L.) is a measure of significance among means. If the mean of any treatment is lower than the L.S.L. of any higher mean then it is significantly lower than that mean at the .05 level (Duncan, 1955).

because of the impossibility of completely randomizing the application of water for each treatment within individual plots. However, it should be mentioned that smaller differences among other completely-randomized effects were significant. Average production on watered plots was 1687.9 gm per plot, compared to 1476.1 gm on unwatered plots. The annual reduction in forage yields (regression coefficient) on watered plots was –481.0 gm compared to –479.7 gm on unwatered plots. This difference between annual reduction rates was not significant by the t test.

Interaction between treatment and application of water was highly significant. Addition of water greatly increased yields from some treatments, whereas no increase was obtained from others. Added water had little effect upon yield of plants clipped only early in the growing season, whereas plants clipped later were materially benefited (Table 3).

In general, added moisture had about the same effect upon plants clipped at either 1-in. or 3-in. stubble height (Table 3). However, in treatments 12 and 8, where the forage was clipped only once (June 1 and June 15, respectively) and treatment 29 where the forage was clipped twice (June 15 and July 1), the plants harvested at 3-in. height were benefited more by additional water than those harvested at 1-in. This would indicate that plants grazed intensively late in the growing season would not respond as well to favorable growing conditions as plants used only moderately late in the season.

EFFECT OF CLIPPING HEIGHT

Total yield from plants clipped at 3 in. was significantly greater than from plants clipped at 1 in.; however, this was not true for all treatments. The control treatment and treatments clipped only once, June 1 or later, produced more when harvested at 1 in. than when harvested at 3 in. (Table 3).

Average yield for plants clipped at 1 in. was 1559.0 gm per plot compared to 1605.0 gm for plants clipped at 3 in. The deleterious effect of increased intensity of clipping was cumulative from year to year. The annual decrease in yield (regression coefficient was –500.6 and –460.8 gm for the 1 in. and 3-in. heights respectively (Table 4). This difference in rate of decrease between the two heights was significant by the "t" test.

EFFECT OF FREQUENCY OF CLIPPING

Average yields from treatments differed significantly, but these differences were significantly influenced by both height of clipping and application of water (Fig. 4 & 5).

Frequency of herbage removal had profound effect upon production of forage. Yield decreased with increased number of clippings when the interval between clippings was varied and season was constant. Plants clipped at weekly, biweekly, and monthly intervals from May 1 to July 1 (treatments 20, 21, and 22) produced an average of 731.2, 975.2, and 1301.7 gm of air-dry herbage for the 5 yrs they were harvested. These yields differed significantly (Table 3). Similarly, treatments 5 & 20, 9 & 23, 13 & 26, and 16 & 28 clipped weekly yielded substantially less than comparable treatments 6 & 21, 10 & 24, 14 & 27, and 17 & 29 which were clipped at 2-week intervals within the same dates.

Yield also decreased with increase in number of clippings when interval between clippings was constant. Such increase, of course, extended the clipping season, but yield decreased regardless of whether season was continued later or started earlier in the growing season. Treatments 5, 9, 13, and 16 clipped at weekly intervals beginning April 15 for a total of 9, 7, 5, and 3 times produced 650.8, 895.5, 1467.9, and 2080.0 gm of forage, respectively.

TABLE 4. Average air dry herbage per plot (10 plants) for plants clipped at various frequencies and at various dates for 5 yrs.

Treatment number	Clipping date*	Clipping interval	Clipping frequency	Yield (grams)						Regression coefficient
				1948†	1949	1950	1951	1952	1953	
			times							
43	——	——	——	3134	3532	3619	3495	2201	2482	−198
19	April 15	——	1	3020	3213	3082	2968	1487	1982	−283
18	May 1	——	1	3079	2853	2564	2331	1638	1513	−316
15	May 15	——	1	3011	2952	2503	2120	1413	1223	−376
12	June 1	——	1	3070	3540	2328	2057	1401	976	−463
8	June 15	——	1	2945	4040	2531	2101	1620	994	−471
4	July 1	——	1	3044	4500	3051	2635	1824	1403	−449
1	April 15 to July 1	One week	11	3003	1111	633	521	312	241	−440
5	April 15 to June 15	One week	9	3090	1271	713	594	373	300	−452
9	April 15 to June 1	One week	7	3072	1345	979	1122	612	418	−414
13	April 15 to May 15	One week	5	2959	2053	1841	1503	1124	817	−373
16	April 15 to May 1	One week	3	3004	2717	2296	2312	1623	1451	−298
20	May 1 to July 1	One week	9	3137	1446	909	675	360	263	−482
23	May 15 to July 1	One week	7	3067	2021	1166	1051	603	445	−472
26	June 1 to July 1	One week	5	2913	2816	1998	1731	1100	754	−438
28	June 15 to July 1	One week	3	2974	3714	2558	2372	1673	1256	−402
30	May 1 to June 15	One week	7	2835	1746	1208	938	547	367	−437
33	May 1 to June 1	One week	5	3042	2148	1599	1221	723	525	−465
35	May 15 to June 15	One week	5	2945	2606	1710	1517	908	617	−457
37	May 1 to May 15	One week	3	3054	2488	2285	1795	1236	1037	−387
39	May 15 to June 1	One week	3	3063	2799	1933	1963	1108	935	−423
41	June 1 to June 15	One week	3	3078	3696	2540	2106	1438	1103	−461
2	April 15 to July 1	Two weeks	6	3071	1654	1058	821	482	392	−463
6	April 15 to June 15	Two weeks	5	2984	1785	1335	947	548	418	−458
10	April 15 to June 1	Two weeks	4	3255	1970	1346	1153	851	476	−471
14	April 15 to May 15	Two weeks	3	2955	2045	1758	1502	1075	875	−366
17	April 15 to May 1	Two weeks	2	3035	2815	2538	2394	1796	1596	−280
21	May 1 to July 1	Two weeks	5	3097	1908	1242	903	476	346	−497
24	May 15 to July 1	Two weeks	4	3116	2227	1542	1271	735	505	−481
27	June 1 to July 1	Two weeks	3	2974	3058	1967	1682	1127	739	−466
29	June 15 to July 1	Two weeks	2	3012	3834	2391	2171	1486	1055	−460
31	May 1 to June 15	Two weeks	4	3188	2125	1545	1171	721	441	−495
34	May 1 to June 1	Two weeks	3	3016	2218	1548	1293	857	566	−448
36	May 15 to June 15	Two weeks	3	3025	2794	2037	1622	925	633	−485
38	May 1 to May 15	Two weeks	2	3224	2510	2183	1699	1241	1021	−413
40	May 15 to June 1	Two weeks	2	3189	2932	2117	1982	1222	919	−448
42	June 1 to June 15	Two weeks	2	3011	3253	2265	2119	1439	962	−427
11	April 15 to June 1	Three weeks	3	3055	2117	1534	1295	943	570	−437
25	May 15 to July 1	Three weeks	3	3014	2420	1510	1216	761	527	−475
32	May 1 to June 15	Three weeks	3	3019	2155	1492	1249	892	545	−443
7	April 15 to June 15	Three weeks	3	3081	2372	1715	1392	887	640	−458
22	May 1 to July 1	Four weeks	3	3102	2493	1526	1262	742	474	−502
3	April 15 to July 1	Five weeks	3	3164	2351	1479	1259	815	536	−485
Average				3046	2550	1865	1617	1055	822	−480
1 inch clipping height (average)				3069	2596	1825	1603	1017	755	−500.6‡
3 inch clipping height (average)				3030	2505	1905	1632	1093	890	−460.8‡
Unwatered plots (average)				2860	2505	1758	1527	867	723	−479.7‡
Watered plots (average)				3232	2595	1972	1708	1243	922	−481.0‡

*All plants were also clipped once during October and weight of this herbage is included here.
†During the fall of 1948 all plants were clipped and weighed for the first time. Differences among treatments represent only normal variability.
‡The t value for comparing regression coefficients for 1- and 3-inch heights is 56.15 which indicates that the difference between them is highly significant. For watered and unwatered plots the t value is 1.84 which is not significant.

EFFECT OF DATE OF CLIPPING

Date of herbage removal also was an important factor affecting forage production. Clipping every week early in the growing season decreased the yield less from year to year than clipping every week late in the season. Plants clipped every week in early season (treatments 5, 9, 13, and 16) decreased from an average of 3031 gm in 1948 to 746.5 in 1953 with an average regression coefficient of −384.7 gm (Table 4). Plants clipped every week late in the season (treatments 20, 23, 26, and 28) decreased from 3023 gm in 1948 to 679.5 in 1953, with an average regression coefficient of −448.8 gm. Late clipping produced more forage the first 2 yrs than early clipping. However, during the last 3 yrs of treatment, plants clipped during late season declined in production more rapidly and were producing less forage at the end of the experiment than the early clipped plants (Table 4).

Clipping at 2 to 3 week intervals at the beginning

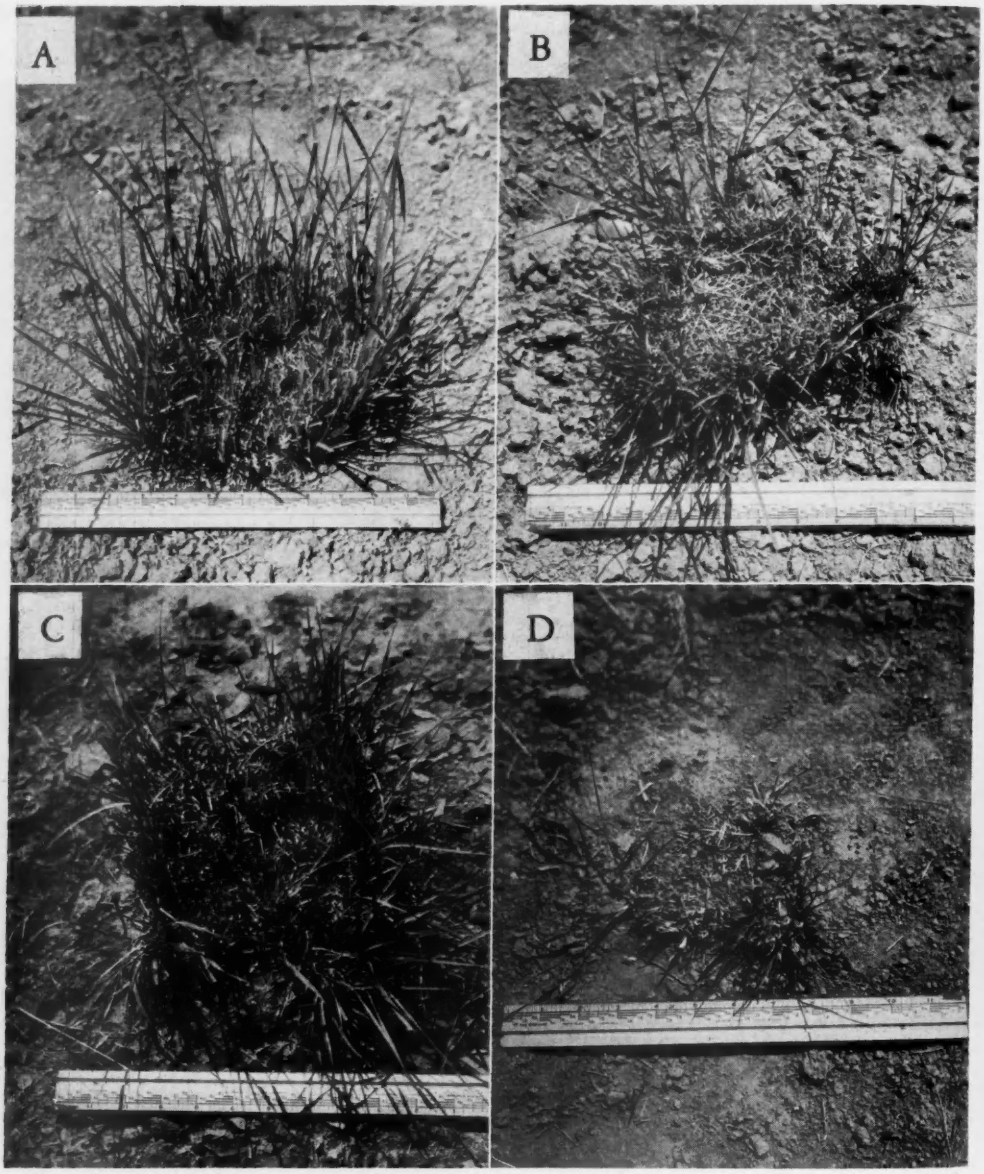

FIG. 4. Crested wheatgrass plants clipped weekly from April 15 to July 1 for 2 yrs (pictures taken July 14). (A) clipped at 3 in. height on watered plot, (B) clipped at 3 in. height on unwatered plot, (C) clipped at 1 in. height on watered plot and (D) clipped at 1 in. height on unwatered plot.

of the growing season resulted in little difference in yield compared to clipping at the same intervals late in the season.

When plants were clipped only once during the growing season, late season (June 15 & July 1) or early season clipping (April 15 & May 15) produced significantly more dry weight than mid-season clipping (May 15 or June 1). The same was true when plants were harvested more than once. Treatments 13 and 14 clipped April 15 to May 15 at weekly and biweekly intervals, respectively, produced more forage during the five years than comparable treatments 33 and 34 clipped May 1 to June 1, but less than treatments 26 and 27 clipped June 1 to July 1. A similar comparison can be made for treatments 16, 37, and 28 clipped at weekly intervals in early, mid, and late growing season, respectively. Again it should be noted that even though early-

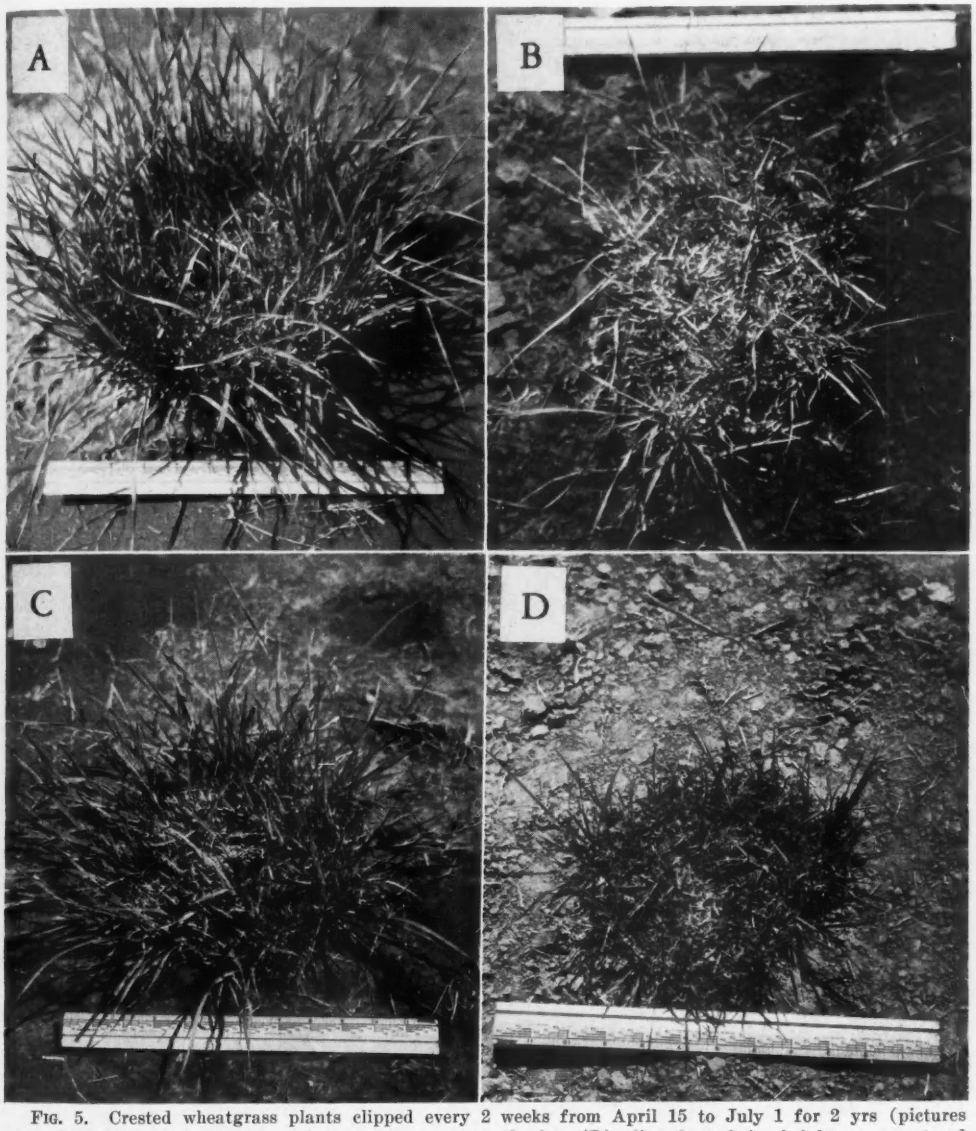

FIG. 5. Crested wheatgrass plants clipped every 2 weeks from April 15 to July 1 for 2 yrs (pictures taken July 14). (A) clipped at 3 in. height on watered plot, (B) clipped at 3 in. height on unwatered plot, (C) clipped at 1 in. height on watered plot, and (D) clipped at 1 in. height on unwatered plot.

harvested plants produced a total yield for the 5 yrs lower than late-harvested plants, the plants clipped early were producing more herbage at the end of the experiment than plants clipped late. Plants clipped in mid-season were producing the least forage after five years of treatment. During the 5 yrs they also produced the least total forage and had the greatest annual decrease in yield.

GROWTH AFTER HARVESTING

Initial spring growth in crested wheatgrass arises from the lowermost nodes of the previous years' stem. Leaf primordia develop on the sides of the shoot apex. Developing leaves upon the shoot rapidly telescope out from within the sheath of the next lower leaf. This results both from growth of the leaf and from elongation of the internode. As soon as a leaf emerges from the enclosing sheath and unrolls, the basal meristem of that leaf becomes inactive. A leaf whose tip is harvested after the leaf fully emerges from the sheath does not elongate or grow further (Cook & Stoddart 1953).

When the stem is harvested anywhere below the

TABLE 5. Analysis of variance of forage production for crested wheatgrass harvested at various frequencies and intensities on watered and unwatered plots for 5 yrs.

Source of variation	Degrees of freedom	Mean squares
Water (H_2O)	1	19,298,157
Error (a) (reps. within H_2O)	2	1,429,056
Treatments (tr.)	42	13,300,551†
Tr. x H_2O	42	432,202†
Height (ht.)	1	908,178*
Ht. x H_2O	1	253,740
Ht. x tr.	42	474,398†
Ht. x tr. x H_2O	42	129,301
Error (b)	170	159,947
Years	4	161,117,097†
Years x H_2O	4	918,113†
Years x tr.	168	442,795†
Years x ht.	4	626,535†
Years x tr. x H_2O	168	45,134
Years x ht. x H_2O	4	684,447†
Years x ht. x tr.	168	67,262†
Error (c)	856	29,106

*Significant at .05 level. †Significant at .01 level.

uppermost node of the culm, axillary leaf buds at the base of the culms are stimulated and new shoots begin growth to replace the original stems. However, when culms are harvested above the uppermost node they continue to grow, but the growth may be composed of virtually a leafless stem (Fig. 6).

When plants are harvested below the uppermost node so that regrowth originates from newly-stimulated tiller or basal buds, available forage growth is substantially reduced.

Plants clipped May 1 displayed regrowth of two types, (1) from tiller buds, and (2) from continued elongation of the stem. Growth on May 15 from plants clipped May 1 showed that regrowth from tiller buds averaged 3 in. above the crown compared to continued elongation of stems, which averaged 5 in.

EFFECT OF WATER

Growth on watered plots was substantially more rapid than on unwatered plots if the plants were clipped more than once during the growing season. The influence of additional water upon growth and production generally was more pronounced on plants clipped late in the growing season. Rate of growth was increased more by additional water as intensity and frequency of clipping increased, Table 6). Regrowth late in the growing season is more dependent on additional moisture than early season growth. Fall yield from plants clipped only in early spring (treatments 19 & 15) was increased but slightly by additional water. However, treatment 8, which was clipped once late in the growing season, produced 52% more herbage in the fall when watered (Table 6).

Plants clipped at weekly, biweekly, and monthly intervals (treatments 5, 6, and 7) produced 144, 95, and 60% more herbage by fall if watered (Table 6).

FIG. 6. Crested wheatgrass displaying characteristic growth after being clipped at 1-in. height. The outer culm nearer the parameter of the plant was clipped somewhat higher than the more central one and produced a normal head and 3 cropped leaves. Inner culms produced no leaf blades and only partially developed seed heads.

Plants clipped only once at 1 in. on May 15 (treatment 15) produced 14% more herbage by fall if watered. When clipped at 3 in., the difference was only 8%. Plants clipped at 1 in. at weekly intervals for 2 months (treatment 5) produced 227% more forage in the fall when watered and plants clipped at 3 in. produced 115% more.

EFFECT OF FREQUENCY AND INTENSITY OF CLIPPING

Normally the control plants were about 4 to 5 in. high and had produced 3 leaves by April 15 when clipping started. These plants were in full anthesis or caryopses were in early milk stage of development by the first of July, when clipping ceased.

In general, plants clipped at 1-in. height were more retarded in rate of growth than plants clipped at 3-in. heights, and, consequently, were more delayed in reaching various stages of development after clipping ceased. This was true, generally, for regrowth from crown buds as well as continued growth and elongation of initial stems. The greater the frequency of clipping, the greater the retardation of growth rate between 1 and 3-in. clipping. Plants

TABLE 6. Average grams of air-dry herbage produced per year per plot (10 plants) for selected treatments clipped for 5 yrs at various dates at 1- and 3-in. heights on watered and unwatered plots.

Treatment number	Moisture	Clipping heights	4/15	4/22	5/1	5/7	5/15	5/22	6/1	6/7	6/15	6/22	7/1	10/1	Total
43	Unwatered	1												3535.5	3535.5
		3												2912.4	2912.4
	Watered	1												3133.8	3133.8
		3												2683.2	2683.2
		Avg.												3066.2	3066.2
19	Unwatered	1	225.5											2595.5	2821.0
		3	147.6											2785.8	2933.4
	Watered	1	172.2											1886.9	2059.1
		3	123.8											2249.7	2373.5
		Avg.	167.5											2379.4	2546.8
15	Unwatered	1					708.2							1128.0	1836.2
		3					739.1							1430.3	2169.4
	Watered	1					775.4							1283.7	2059.1
		3					663.7							1442.2	2105.9
		Avg.					721.6							1321.0	2042.7
8	Unwatered	1									1996.3			416.8	2413.1
		3									1811.0			235.5	2046.5
	Watered	1									1775.0			568.5	2343.5
		3									1804.3			423.7	2228.0
		Avg.									1846.6			411.1	2257.8
7	Unwatered	1	203.1				403.0				272.4			455.6	1334.1
		3	120.1				398.0				407.6			317.8	1243.5
	Watered	1	198.1				347.4				262.7			705.3	1513.5
		3	126.5				369.7				437.6			581.4	1515.2
		Avg.	161.9				379.5				345.1			515.0	1401.6
6	Unwatered	1	139.3		111.5		70.8		47.5		24.0			283.1	676.2
		3	119.2		167.4		143.3		123.0		48.0			306.4	907.3
	Watered	1	212.9		183.8		106.6		66.3		31.9			569.1	1170.6
		3	143.6		183.2		155.9		158.9		50.9			582.3	1274.8
		Avg.	153.7		161.5		119.1		98.9		38.7			435.2	1007.2
5	Unwatered	1	94.3	43.2	47.8	12.2	17.7	12.2	8.8	8.6	5.0			77.4	327.2
		3	99.0	67.1	80.7	57.2	54.4	35.7	52.1	31.4	15.7			212.0	705.3
	Watered	1	107.7	47.9	51.2	25.0	23.0	17.8	17.5	10.8	10.3			251.7	562.9
		3	120.7	71.4	83.5	61.0	71.8	45.2	51.4	24.9	21.2			456.7	1007.8
		Avg.	105.4	57.4	65.8	38.8	41.7	27.7	32.4	18.9	13.0			249.4	650.8
36	Unwatered	1					955.2		63.2		103.0			552.0	1673.4
		3					616.1		181.2		65.4			577.0	1439.7
	Watered	1					771.9		69.3		97.7			832.2	1771.1
		3					585.0		151.8		95.2			694.6	1526.6
		Avg.					732.0		116.4		90.3			663.9	1602.7
31	Unwatered	1			431.0		97.7		66.0		46.4			392.3	1033.4
		3			365.1		187.1		134.2		48.6			422.8	1157.8
	Watered	1			424.2		122.2		73.7		48.4			641.7	1310.2
		3			341.6		170.9		130.8		56.8			602.1	1302.2
		Avg.			390.5		144.5		101.2		50.0			514.7	1200.9
24	Unwatered	1					636.4		49.7		81.8		77.8	182.3	1028.0
		3					596.9		168.7		78.3		101.7	295.0	1240.6
	Watered	1					708.5		66.3		95.0		85.7	495.4	1450.9
		3					527.6		134.3		79.4		108.3	456.5	1306.1
		Avg.					617.3		104.7		83.4		93.4	357.3	1256.4
21	Unwatered	1			314.4		85.9		51.5		35.7		27.7	195.5	710.7
		3			245.9		148.3		113.9		39.0		47.2	165.9	760.2
	Watered	1			383.9		114.5		154.2		38.8		48.5	433.1	1173.0
		3			322.5		177.9		143.7		45.5		76.1	491.3	1257.0
		Avg.			316.7		131.6		115.8		39.7		49.9	321.4	975.2

TABLE 7. Average height and vigor in autumn of plants clipped at various seasons and frequencies at a height of 1 and 3 in., and on watered and unwatered plots.*

Treatment number	Clipping interval	Clipping date	Average height	Lower significant limit†	Average vigor class‡	Lower significant limit†
			(inches)			
43	Control	Oct. 1	32.0	30.2	1.1	—
19	Once	April 15	31.4	29.6	1.4	1.0
18	Once	May 1	27.8	26.0	1.6	1.3
15	Once	May 15	22.0	20.2	2.3	2.0
12	Once	June 1	15.3	13.5	3.0	2.6
8	Once	June 15	9.4	7.7	3.4	3.0
4	Once	July 1	5.9	4.4	3.8	3.4
1	Weekly	April 15-July 1	5.9	4.5	5.4	5.0
5	Weekly	April 15-June 15	8.7	7.0	5.0	4.6
9	Weekly	April 15-June 1	12.2	10.4	3.9	3.5
13	Weekly	April 15-May 15	20.0	18.1	2.5	2.1
16	Weekly	April 15-May 1	26.3	24.5	1.7	1.3
20	Weekly	May 1-July 1	5.7	—	5.3	4.9
23	Weekly	May 15-July 1	7.0	5.5	4.9	4.5
26	Weekly	June 1-July 1	9.6	7.9	3.9	3.5
28	Weekly	June 15-July 1	9.1	7.4	3.6	3.2
30	Weekly	May 1-June 15	10.7	9.0	4.4	4.0
33	Weekly	May 1-June 1	14.8	13.0	3.6	3.2
35	Weekly	May 15-June 15	13.8	12.0	3.4	3.0
37	Weekly	May 1-May 15	20.7	18.9	2.4	2.0
39	Weekly	May 15-June 1	19.3	17.5	2.5	2.1
41	Weekly	June 1-June 15	14.9	13.1	3.0	2.6
2	Biweekly	April 15-July 1	7.6	6.0	4.8	4.4
6	Biweekly	April 15-June 15	11.2	9.4	4.1	3.7
10	Biweekly	April 15-June 1	14.5	12.7	3.5	3.1
14	Biweekly	April 15-May 15	19.7	17.9	2.6	2.2
17	Biweekly	April 15-May 1	26.4	24.6	1.8	1.4
21	Biweekly	May 1-July 1	8.0	6.3	4.9	4.5
24	Biweekly	May 15-July 1	8.0	6.4	4.7	4.3
27	Biweekly	June 1-July 1	11.4	9.7	4.0	3.6
29	Biweekly	June 15-July 1	7.5	5.9	3.7	3.3
31	Biweekly	May 15-June 15	12.0	10.2	3.9	3.5
34	Biweekly	May 1-June 1	15.8	14.0	3.2	2.8
36	Biweekly	May 15-June 15	14.2	12.4	3.4	3.0
38	Biweekly	May 1-May 15	21.3	19.5	2.6	2.2
40	Biweekly	May 15-June 1	19.5	17.7	2.5	2.1
42	Biweekly	June 1-June 15	14.2	12.4	3.1	2.7
11	Triweekly	April 15-June 1	13.8	12.0	3.3	3.0
25	Triweekly	May 15-July 1	7.9	6.3	4.4	4.0
32	Triweekly	May 1-June 15	12.3	10.5	3.5	3.1
7	Monthly	April 15-June 15	12.4	10.6	4.0	3.6
22	Monthly	May 1-July 1	10.1	8.4	4.3	3.9
3	5-weekly	April 15-July 1	8.1	6.4	4.4	4.0
Unwatered		1 inch	12.5		3.9	
		3 inch	14.8		3.5	
Average			13.6		3.7	
Watered		1 inch	14.2		3.3	
		3 inch	16.1		3.1	
Average			15.1		3.2	
Average 1-inch clipping height			13.3		3.6	
Average 3-inch clipping height			15.4		3.3	

*Measurements were made in the fall after the plants had been clipped for two years, again after four years of clipping, and a third time after five years of clipping.
†Any mean having a lower value than the L.S.L. of any other mean is significantly lower than that mean at the 5% level (Duncan 1955).
‡1 is maximum vigor and 7 is minimum vigor.

clipped at 1 in. on July 1 produced an average of 3 in. of new growth by July 22, whereas plants clipped at 3 in. produced an average of 5 in. of new growth. Likewise, frequency of clipping materially affected subsequent rate of growth. Plants clipped weekly at 3 in. from April 15 to May 15 produced an average of 3 in. of new growth by June 1, whereas plants clipped biweekly at 3 in. produced an average of 7 in. of new growth. These differences were more pronounced on unwatered plots than on watered plots. With each additional clipping, the rate of growth was decreased and development delayed. Plants clipped frequently and intensively during June failed to produce mature seed by October 1.

On May 15, plants clipped after an interval of one month (treatment 7) yielded an average of 379.5 gm of new forage. Plants clipped twice during the same interval (treatment 6) and plants clipped 3

times (treatment 5) produced 280.6 and 203.7 gm of new forage, respectively (Table 6).

Plants clipped weekly at 1 in. (treatment 5) produced an average of 134.0 gm of forage from April 15 to May 15 and were 2 in. high when clipped on May 15. Plants, clipped weekly at 3 in., produced 273.5 gm of forage and were 5 in. high on May 15.

EFFECT OF DATE OF CLIPPING

The later the date of clipping, the longer the delay in appearance of regrowth from tiller buds. Regrowth on plants clipped early in the spring (May 1) was about 3 in. above the crown 2 weeks later; whereas, plants clipped later in the spring (June 1 or later), had only about 1 in. of regrowth above the crown two weeks later.

VIGOR AND HEIGHT

Vigor of plants was determined in the fall of 1950 after the plants had been under treatment for 2 yrs, again in 1952 after 4 yrs, and again in 1953 after 5 yrs. Vigor was based upon the number and leafiness of seed culms. The vigor was classified from 1 to 7 with 1 representing maximum as displayed by the control plants and 7 representing the minimum. Height of culms was determined by measuring the tallest seed stalk in each quarter of the grass clump.

EFFECT OF WATER

The application of water significantly affected both height and vigor of the plants (Tables 7 & 8). Plants that received additional moisture averaged about 2 in. taller and were measurably more vigorous (Table 7).

TABLE 8. Analysis of variance for data presented in Table 7 for height and vigor of crested wheatgrass plants clipped at various intensities and frequencies.

Source of variation	Degrees of freedom	Mean Squares	
		Height	Vigor class
Water (H_2O)	1	1,141.59*	123.56*
Error (a) (reps. within H_2O)	2	15.56	36.49
Treatments (tr.)	42	2,328.48†	55.65†
Tr. x H_2O	42	33.97*	1.87†
Height (ht.)	1	2,325.82†	41.59†
Ht. x H_2O	1	26.30	2.87*
Ht. x tr.	42	34.48†	2.99†
Ht. x tr. x H_2O	42	9.46	.73
Error (b)	170	12.44	.69
Years	4	5,237.70†	54.76†
Years x H_2O	4	25.64	86.38†
Years x tr.	168	33.30†	1.10
Years x ht.	4	6.64	.51
Years x tr. x H_2O	168	7.28	.69
Years x ht. x H_2O	4	6.21	.39
Years x ht. x tr.	168	5.84	.34
Error (c)	856	12.50	1.12

*Significant at .05 level. †Significant at .01 level.

EFFECT OF CLIPPING HEIGHT

Plants clipped at 3 in. averaged about 3 in. taller in the fall than plants clipped at 1 in. This was largely a result of closer clipping requiring regrowth from crown buds, whereas at the higher clipping height many of the culms were a result of continued elongation of the internodes.

The average vigor in the fall for plants clipped at 1 in. was significantly lower than for those clipped at 3 in. (Tables 7 & 8). In 1953, the plants clipped at 1 in. had a vigor class of 3.6 compared to 3.3 for plants clipped at 3 in.

Both height and vigor in the fall for plants watered and unwatered and for plants clipped at 1 in. and at 3 in. decreased from the beginning of the experiment to the end regardless of clipping treatments. However, the decrease was not as great for plants receiving additional water or for plants clipped at 3 in.

EFFECT OF FREQUENCY AND DATE OF CLIPPING

Date and frequency of clipping significantly affected both height and vigor of plants (Tables 7 & 8).

Increased frequently of clipping reduced vigor and in general decreased fall height. Plants clipped weekly had an average vigor index of 4.2, compared to biweekly treatments which had an average vigor index of 3.7. In like manner, fall height of weekly clipped plants was lower than that of biweekly clipped plants.

Season of clipping and date of cessation of clipping were important factors that affected height and vigor. Plants clipped only once during the growing season showed that as the date of clipping was delayed, stature and vigor of the plant were reduced. Plants clipped on April 15 (treatment 19) were about 31 in. tall by fall at the end of the experiment and had excellent vigor. Plants clipped on July 1 (treatment 4) were only 6.3 in. high in the fall and vigor was reduced to class 4.7. In most cases, height by the end of the year was reduced as date of cessation of clipping was delayed regardless of frequency or interval of clipping.

SEED PRODUCTION

The number of spikes per plant was counted on 15 selected treatments. Counts were made at time of seed maturity in 1949; again in 1953; and again in 1954 after treatments had been terminated for a full year.

All of the spikes produced in one quarter of the clump were collected from randomly selected mature plants to determine the number of filled caryopses per head. Caryopses were considered filled when 50% or more of the seed coat formed by the lemma and palea appeared filled. This somewhat arbitrary determination was made by examing the caryopses over a light-table. A composite was obtained from counts made by three individuals for each treatment and each collection.

EFFECT OF WATER

The number of spikes per plant was higher, in most cases, on watered than on unwatered plots. This was especially true when cessation of clipping

TABLE 9. Average number of spikes per plant, filled caryopses per spike, viable seed per plant, and percent germination of seed for crested wheatgrass plants clipped at 1-in. and 3-in. stubble height on watered and unwatered plots when clipped at various frequencies and various seasons throughout the growing season, after 1 yr of treatment (1949), after 5 yrs of treatment (1953), and again in 1954 one yr after treatment ceased.

Treatment	Interval	Date Clipped	Spikes Per Plant			Filled Caryopses Per Spike			Viable Seed Per Plant			Percent Germination*		
			1949	1953	1954	1949	1953	1954	1949	1953	1954	1949	1953	1954
43	——	——	398.6	327.6	49.8	23.3	19.9	34.9	8,373.2	2,914.4	1,724.5	93.2	60.1	93.6
			(335.3)†	(270.8)	(35.2)	(16.5)	(13.4)	(——)	(6,932.5)	(1,830.7)	(770.5)			
19	——	April 15	283.9	204.8	59.8	20.0	11.3	30.0	5,051.6	1,181.7	1,421.4	92.4	49.7	77.4
			(221.0)	(148.6)	(45.0)	(13.3)	(4.9)	(——)	(3,627.8)	(117.1)	(481.7)			
18	——	May 1	247.6	226.9	40.7	24.0	19.5	45.4	5,092.2	2,793.4	1,767.8	93.2	63.1	93.2
			(186.0)	(170.4)	(26.3)	(17.2)	(13.0)	(——)	(3,659.9)	(1,716.1)	(808.1)			
15	——	May 15	257.5	145.0	51.6	18.2	15.3	42.8	3,919.8	1,387.7	2,004.7	93.6	55.1	91.3
			(195.3)	(89.3)	(36.9)	(11.5)	(8.8)	(——)	(2,504.5)	(316.8)	(1,033.6)			
12	——	June 1	181.8	69.2	36.7	12.2	3.0	41.9	2,070.6	75.8	1,111.5	93.7	34.8	91.5
			(121.1)	(14.7)	(22.6)	(5.5)	(——)	(——)	(668.0)	(——)	(211.8)			
8	——	June 15	86.7	3.5	37.8	3.9	0.1	35.8	280.9	.5	1,233.6	80.9	54.9	88.9
			(35.1)	(——)	(23.6)	(——)	(——)	(——)	(——)	(——)	(311.0)			
4	——	July 1	5.9	0.0	29.8	0.1	0.0	35.4	.4	0.0	1,063.1			93.4
			(——)	(——)	(16.7)	(——)	(——)	(——)	(——)	(——)	(161.0)			
7	Four weeks	April 15 to June 15	181.5	22.3	33.1	5.7	2.2	39.1	926.5	27.8	1,192.7	91.2	27.8	92.5
			(121.4)	(——)	(19.2)	(——)	(——)	(——)	(——)	(——)	(281.6)			
6	Two weeks	April 15 to June 15	143.9	0.0	16.5	6.1	0.0	27.5	638.8	0.0	453.0	89.1	——	84.5
			(85.3)	(——)	(——)	(——)	(——)	(——)	(——)	(——)	(——)			
5	One week	April 15 to June 15	94.4	0.0	22.6	2.2	0.0	24.6	141.2	0.0	675.1	82.8	——	94.2
			(40.0)	(——)	(10.6)	(——)	(——)	(——)	(——)	(——)	(——)			
42	Two weeks	June 1 to June 15	137.5	134.5	42.2	8.0	3.4	49.1	944.9	225.4	1,953.9	85.4	49.1	94.2
			(81.3)	(79.2)	(27.7)	(1.4)	(——)	(——)	(——)	(——)	(988.5)			
36	Two weeks	May 15 to June 15	264.7	103.4	39.5	4.0	2.0	25.6	875.6	52.7	1,101.8	85.5	30.2	85.6
			(202.2)	(48.4)	(25.2)	(——)	(——)	(——)	(——)	(——)	(168.8)			
31	Two weeks	May 1 to June 15	146.3	59.8	32.4	5.8	2.5	44.0	781.6	53.1	1,514.2	84.0	39.9	91.1
			(86.9)	(5.8)	(18.7)	(——)	(——)	(——)	(——)	(——)	(507.1)			
24	Two weeks	May 15 to July 1	184.8	23.7	30.8	8.8	1.7	51.1	1,430.6	36.6	1,554.1	91.1	38.3	94.5
			(123.5)	(——)	(17.4)	(2.2)	(——)	(——)	(36.5)	(——)	(537.7)			
21	Two weeks	May 1 to July 1	143.9	5.6	27.2	3.7	.3	37.4	502.2	4.2	1,023.1	90.1	43.7	88.5
			(86.3)	(——)	(14.5)	(——)	(——)	(——)	(——)	(——)	(140.5)			
Unwatered		1 inch	169.3	85.1	30.4	9.5	5.0	34.8	2,052.9	610.4	1,094.6	88.9	43.7	91.4
		3 inch	181.2	90.2	36.3	11.4	6.0	38.1	2,021.3	690.2	1,201.3	89.4	43.6	91.4
		Average	175.3	87.6	33.3	10.4	5.5	36.4	2,037.1	650.3	1,148.0	89.1	43.6	91.4
Watered		1 inch	186.2	80.7	38.8	8.3	5.2	38.7	1,915.0	465.3	1,353.7	90.9	38.8	88.0
		3 inch	199.0	97.8	41.4	9.7	5.6	39.0	2,285.6	568.3	1,519.0	85.8	41.4	90.4
		Average	192.6	89.2	40.1	9.0	5.4	38.8	2,100.3	516.8	1,436.3	87.8	40.1	89.2
Height		1 inch	177.8	82.9	34.6	8.9	5.1	36.8	1,983.9	537.9	1,224.2	89.5	34.6	89.7
		3 inch	190.1	94.0	38.8	10.6	5.8	38.5	2,153.5	629.2	1,360.1	87.5	38.8	90.9

*Chi-square ($\chi 2$) for germination percentages for 1949 was 56.5 among treatments (56 degrees of freedom), 19.98 for 1953 among treatments (40 degrees of freedom) and 56.2 for 1954 among treatments (51 degrees of freedom).

†Figures in parenthesis are lower significant limits which are tests of significance among treatments. Any treatment mean having a lower value than the L.S.I. of any other treatment mean is significantly lower than that mean at the 5% level.

was delayed until late in the growing season (Tables 9 & 10).

The difference in number of filled caryopses per spike on watered plots and unwatered plots was not statistically significant (Table 10). However, in 1954, plants on the unwatered plots produced only 33.3 filled caryopses per spike, whereas plants on watered plots produced 40.1 (Table 9).

EFFECT OF CLIPPING HEIGHT

Plants clipped at 1 in. produced an average of 177.8 spikes per plant in 1949 and only 34.6 in 1954, a year after treatment ceased. Plants clipped at 3 in. produced an average of 190.1 spikes per plant in 1949 and 38.8 in 1954 (Table 9). The differences for the over-all effect of height of clipping were not statistically significant (Table 10). In most treatments, plants clipped at 3 in. produced substantially more spikes than plants clipped at 1 in., but in 1949 plants clipped at 1 in. in treatments 8 and 24 produced more spikes than plants clipped at 3 in.

Height of clipping did not significantly affect the number of filled caryopses per spike; however, plants clipped at 3 in. produced a somewhat greater number.

EFFECT OF FREQUENCY AND DATE OF CLIPPING

Date and frequency of harvesting (treatment) had a significant influence on number of spikes produced (Table 10). As date of clipping was delayed number of spikes produced was decreased. Plants clipped only on April 15 produced an average of 283.9 spikes in 1949, after 1 yr of treatment, and

TABLE 10. Analyses of variance for data presented in Table 8 for spikes per plant, filled caryopses per head, and viable seed per plant for crested wheatgrass plants clipped at various intensities and frequencies on watered and unwatered plots after 1 yr of treatment (1949), after 5 yrs of treatment (1953) and again in 1954 after a year free from treatment.

Source	Degrees of freedom	MEAN SQUARES								
		SPIKES PER PLANT			FILLED CARYOPSES PER SPIKE			VIABLE SEED PER PLANT		
		1949	1953	1954	1949	1953	1954	1949	1953	1954
Site (H_2O)	1	8,976.97	80.85	1,364.17	60.07	.48	175.45	119,694.5	534,387.2	2,494,833.1
Replication (reps.)	1	605.25	1,110.82	251.72	159.39	11.53	3,039.12	1,516,433.4	142,065.1	1,000,867.2
Rep. x H_2O (error a)	1	1,191.33	18,344.72	3.54	21.42	37.19	3.11	2,077,200.8	2,485,469.6	168,300.3
Height (ht)	1	4,564.57	3,677.45	535.09	83.17	14.84	95.94	862,534.7	250,481.7	554,744.0
Treatment (tr)	14	73,153.25†	81,606.56†	1,024.99*	498.68†	422.81†	542.69	47,402,553.8†	8,328,605.2†	1,627,571.8*
H_2O x ht	1	5.25	1,069.83	82.35	2.10	2.19	63.22	1,212,814.0	4,040.3	25,737.1
H_2O x tr	14	15,731.91†	3,041.11	228.96	22.31	9.35	674.79	2,193,691.6	913,959.8	1,456,463.4
Ht x tr	14	10,021.58†	1,053.66	234.72	73.77*	8.50	219.89	6,447,284.9†	319,464.6	1,303,684.9
Tr x H_2O x ht	14	10,561.94†	702.46	230.63	27.70	3.43	800.01	1,928,133.0	961,905.9	2,057,467.1*
Remainder (error b)	58	2,774.96	2,235.47	151.68	32.49	29.90	366.81	1,436,539.2	812,751.8	652,607.1

*Significant at the 5% level. †Significant at the 1% level.

59.8 in 1954 one year after treatment ceased. Plants clipped only on July 1 produced 5.9 spikes in 1949 and 29.8 in 1954. All plants clipped after June 15 produced no seed in the fall of 1953.

Increasing the frequency of harvesting decreased the number of spikes produced. Treatments 5, 6, and 7 clipped weekly, biweekly, and monthly from April 15 to June 15 produced 94.4, 143.9, and 181.5 spikes per plant, respectively, during 1949 (Table 9).

Season and frequency of clipping significantly affected the number of filled caryopses produced per spike during the years clipping occurred (Tables 9 & 10). In 1949 and 1953, the number of filled caryopses per spike was materially decreased by delay in date of harvesting. Plants clipped once on May 1 in 1949 produced an average of 24 filled caryopses per spike, whereas plants clipped July 1 averaged less than 1.

Plants clipped weekly, biweekly, and monthly from April 15 to June 15 (treatments 5, 7, & 7) produced 2.2, 6.1, and 5.7 filled caryopses per spike the first year of treatment and 24.6, 27.5, and 39.1, respectively, in 1954 after a year free from treatment.

Even though plants lost vigor and produced significantly fewer spikes per plant when clipped severely, the number of filled caryopses per spike was not statistically different a year after treatments ceased. (tables 9 and 10).

SEED GERMINATION

Germination was determined for each seed collection. Four samples of 100 seeds were tested for each treatment at each height and under each moisture condition. Thus, germination percentages (Table 9) are based on the average of 1600 filled caryopses for each treatment. Viable seed per plant was calculated by multiplying filled caryopses per plant by percent germination.

Germination was not significantly different among treatments when tested by chi-square for any of the three years. Apparently, if vigor of the plant is sufficient so that the caryopses is filled, then it is likely to be viable. However, some treatments were low under both watered and unwatered conditions and under both 1-in. and 3-in. clipping height. It was noted that caryopses from these plants were not as large as those from the unclipped plants or plants with higher germination. It can be theorized, then, that vitality of the seedling from such caryopses may be reduced because of lower food reserve in the seed.

The number of viable seed per plant is a reflection of number of spikes per plant and number of filled caryopses per spike. Frequency and season of clipping were the most influential factors affecting viable seed production. Viable seed decreased as frequency of clipping increased and as date of clipping was delayed. Plants clipped once on April 15 (treatment 19) produced 5,051.6 viable seeds per plant in 1949, and 1,421.4 in 1954. Plants clipped once on July 1 (treatment 4) produced only 0.4 viable seed per plant in 1949 and 996.7 in 1954. Plants clipped at weekly, biweekly, and monthly intervals from April 15 to June 15 (treatments 5, 6 & 7) produced 141.2, 638.8, and 926.5 viable seed per plant in 1949; and 675.1, 453.0, and 1,192.7, respectively, in 1954 (Table 9).

NUTRIENT CONTENT OF FORAGE

Herbage from selected treatments was analyzed for total protein, ether extract, ash, lignin, cellulose, other carbohydrates, calcium, and phosphorus. The percentages of each constituent at each sampling date were averaged and these percentages were not weight-

TABLE 11. Chemical content of crested wheatgrass herbage clipped five years at various frequencies and intensities on watered and unwatered plots. These figures are unweighted averages of the composition at each date clipped.

Treatment number	Clipping interval and date*	Protein	Ether extract	Lignin	Cellulose	Other carbohydrates	Ash	Calcium	Phosphorus	Digestible protein	Digestible organic matter	T. D. N.
						(percent)						
43	—	2.7	2.8	9.2	37.4	42.1	6.3	.33	.078	0	50.8	52.7
		(—)	(—)	(8.8)	(35.2)	(41.1)	(—)	(—)	(—)			
19	April 15	16.2	3.2	6.4	27.6	38.5	8.6	.41	.244	11.6	61.7	64.4
		(15.9)†	(1.1)	(6.0)	(25.5)	(37.5)	(8.3)	(.23)	(.240)			
18	May 1	14.6	3.2	6.8	28.6	38.6	9.3	.38	.221	10.2	59.5	62.2
		(14.3)	(1.1)	(6.4)	(26.4)	(37.6)	(8.9)	(.21)	(.217)			
15	May 15	12.2	3.7	6.6	28.8	40.4	9.1	.37	.201	7.9	60.4	63.5
		(11.9)	(1.4)	(6.2)	(26.6)	(39.4)	(8.7)	(.21)	(.197)			
12	June 1	11.0	3.7	6.7	2).9	40.2	9.0	.42	.197	6.9	60.2	63.2
		(10.7)	(1.4)	(6.3)	(27.7)	(39.2)	(3.6)	(.24)	(.193)			
8	June 15	9.9	3.7	7.0	31.1	40.3	8.9	.43	.185	5.9	58.8	61.8
		(9.6)	(1.4)	(6.6)	(28.9)	(39.3)	(8.5)	(.25)	(.181)			
4	July 1	10.8	4.2	7.4	30.9	37.5	9.7	.51	.186	6.8	56.8	60.2
		(10.5)	(1.9)	(7.0)	(28.7)	(36.5)	(9.3)	(.32)	(.182)			
7	Monthly	19.9	3.7	5.8	26.2	34.8	10.3	.44	.293	15.2	63.2	66.4
	April 15 to June 15	(19.6)	(1.4)	(5.4)	(24.2)	(33.9)	(9.9)	(.26)	(.289)			
6	Biweekly	24.0	3.5	5.0	24.8	31.9	11.0	.47	.351	19.3	65.9	69.2
	April 15 to June 15	(23.7)	(1.2)	(4.7)	(23.0)	(31.0)	(10.6)	(.28)	(.347)			
5	Weekly	26.6	3.2	4.9	24.6	29.6	11.9	.52	.391	21.9	65.7	68.7
	April 15 to June 15	(26.3)	(1.1)	(—)	(—)	(—)	(11.5)	(.33)	(.387)			
42	Biweekly	13.8	3.5	6.3	29.0	36.6	11.3	.47	.262	9.4	60.3	63.3
	June 1 to June 15	(13.5)	(1.2)	(5.9)	(26.8)	(35.6)	(10.9)	(.28)	(.258)			
36	Biweekly	18.1	3.4	5.5	27.2	35.7	10.7	.43	.314	13.4	64.0	67.0
	May 15 to June 15	(17.8)	(1.2)	(5.1)	(25.1)	(34.8)	(10.3)	(.25)	(.310)			
31	Biweekly	22.0	3.4	5.3	26.3	32.7	11.0	.45	.351	17.2	64.6	67.5
	May 1 to June 15	(21.7)	(1.2)	(4.9)	(24.3)	(31.8)	(10.6)	(.26)	(.347)			
24	Biweekly	19.4	3.5	5.5	26.8	34.4	11.1	.45	.319	14.7	63.7	66.9
	May 15 to July 1	(19.1)	(1.2)	(5.1)	(24.7)	(33.5)	(10.7)	(.26)	(.315)			
21	Biweekly	21.8	3.6	5.2	25.1	33.2	11.3	.46	.330	17.0	65.0	68.3
	May 1 to July 1	(21.5)	(1.3)	(4.8)	(23.2)	(32.3)	(10.9)	(—)	(—)			
Unwatered	1 inch	16.9	3.4	6.1	27.4	36.6	10.2	.43	.26	12.6	61.7	64.7
	3 inch	16.1	3.6	6.3	29.0	36.3	9.4	.40	.24	11.7	61.3	64.2
	Average	16.5	3.5	6.2	28.2	36.4	9.8	.42	.25	11.9	61.6	64.6
Watered	1 inch	16.2	3.4	6.2	27.8	36.3	10.6	.46	.27	11.8	60.9	63.9
	3 inch	15.6	3.5	6.3	28.8	36.5	9.6	.44	.26	11.2	61.4	64.4
	Average	15.9	3.5	6.2	28.3	36.4	10.1	.45	.26	11.3	61.2	64.2
Average	1 inch	16.6	3.4	6.1	27.6	36.4	10.4	.45	.26	11.9	61.5	64.4
Average	3 inch	15.8	3.5	6.3	28.9	36.4	9.5	.42	.25	11.3	61.4	64.4

*All plants were clipped on October 1 each year in addition to dates shown.
†Figures shown in parenthesis are the lower significant limit (L.S.L.), a test of significance among treatments. Any treatment mean having a lower value than the L.S.L. of any other treatment mean is significantly lower than that mean at the 5 percent level (Duncan 1955).

ed according to quantity of herbage produced. This average, including the October clipping is shown in Table 11. In addition digestible protein, digestible organic matter, and total digestible nutrients were calculated by formula. Digestible protein was determined by the formula proposed by Mitchell (1942) which shows a relation between protein content of forage and apparent digestibility of protein as follows:

Percent digestibility of protein = 9.159 (% protein − 5).

Protein digestibility as calculated by this formula agrees closely with that determined by field digestion trials made by Cook *et al.* (1956) on crested wheatgrass.

Digestibility of organic matter is associated with lignin content of crested wheatgrass (Cook & Harris 1952, Cook *et al.* 1956) as follows:

Percent digestibility of organic matter = 97.5 + [−4.67 × % lignin]

Total digestible nutrients were determined by a formula from Lofgreen (1953) which is:

Percent total digestible nutrients = % organic matter [.01 + .000125% ether extract in organic matter] [% digestibility of organic matter]

Nutrient content showed no relation to severity of treatment from year to year, but quantity of the various nutrients changed as herbage yield changed.

EFFECT OF WATER

In general, herbage harvested from watered plots had higher percentages of ash, calcium, phosphorus, and cellulose. In a few treatments additional water had a significant effect on still other constituents. The effect of water on other chemical constituents was dependent on clipping treatment. Herbage harvested either late in the growing season or at frequent intervals was higher in protein, digestible organic matter, and total digestible nutrients on unwatered plots than on watered plots. Unwatered plots har-

TABLE 12. Analysis of variance for percent chemical composition of crested wheatgrass clipped at different dates and frequencies at 1- and 3-in. heights and under watered and unwatered conditions for a period of 5 yrs. (See Table 11)

Source	Degrees of freedom	Mean Squares							
		Total protein	Ether extract	Lignin	Cellulose	Other carbohydrates	Ash	Calcium	Phosphorus
Water (H_2O)	1	28.58	.009	.10	.37	.001	6.20	.10565	.01731*
Year x H_2O (error a)	4	11.69	1.523	.72	1.58	25.604	1.14	.02315	.00188
Treatment (tr.)	14	804.72†	2.085†	90.93†	213.94†	265.258†	42.32†	.18309†	.14249†
Height (ht.)	1	38.77†	.982†	1.84*	129.65†	.087	57.86†	.03608	.00824†
Tr. x ht.	14	4.84†	.298†	.85†	14.66†	3.997*	2.30†	.01845	.00096†
Year	4	131.44†	9.519†	.91*	185.66†	1013.019†	18.07†	.64793†	.00028†
Yr. x tr.	56	6.05†	.260†	.85†	9.04†	14.802†	1.55†	.00866	.00100†
Yr. x ht.	4	1.41†	.071	.21	.10	1.870	.83*	.00237	.00064†
Yr. x tr. x ht.	56	1.18†	.115	.35	1.54*	2.775	.81	.00378	.00005
Yr. x tr. x H_2O	56	2.12†	.160	.49	2.09†	3.346*	.26	.00239	.00005
Yr. x ht. x H_2O	4	.61†	.079	.21	1.78	2.653	.28	.00353	.00010
Tr. x H_2O	14	1.77†	.254*	.35	3.22†	2.309	.84†	.01024	.00005†
Ht. x H_2O	1	1.74†	.230	.53	5.06	4.934	.27	.00019	.00008
Tr. x ht. x H_2O	14	2.07†	.175	.38	1.15	3.931*	.45	.00828	.00034†
Yr. x tr. x ht. x H_2O (error b)	56	.15	.107	.33	.88	1.985	.31	.06648	.00004

*Indicates significance at the 5% level. †Indicates significance at the 1% level.

vested once on July 1 and others harvested once on June 15 produced an average of 11.3 and 10.3% protein compared to watered plots which produced 10.4 and 9.7%. Protein for treatment 5, clipped weekly, was 27.5% on unwatered plots and 25.7% on watered plots, whereas plants clipped at monthly intervals (treatment 7) contained 20.5% on unwatered plots and 19.5% on watered plots. Percent protein was higher in herbage from unwatered plots harvested from April 15 to June 15 (treatments 5, 6, & 7) but percent phosphorus was higher on watered plots.

Forage from plants clipped biweekly from April 15 to June 15 (treatment 6) and those clipped biweekly from May 1 to July 1 (treatment 21) was higher in percentage of protein and total digestible nutrients on unwatered plots, whereas herbage from watered plants was higher in lignin, calcium, and phophorus.

EFFECT OF CLIPPING HEIGHT

In general, herbage harvested at three inches contained a higher percentage of cellulose and lignin and a lower percentage of protein than forage harvested at 1 in., regardless of frequency of clipping (Table 11).

Herbage harvested at biweekly intervals from April 15 to June 15 (treatment 6) and from May 1 to July 1 (treatment 21) had a higher percentage of protein, other carbohydrates, calcium, phosphorus, digestible organic matter, and total digestible nutrients when clipped at 1 in. compared to plants clipped at 3 in.

Height of clipping had significant effects upon the percent nutrient content, likely a result of difference in amount of new leafy growth included in the harvested material.

Numerous interactions between height of clipping, season, and frequency of clipping emphasize the interrelationships of these factors in determining yield of nutrients and maintenance of production under different practices of range utilization.

EFFECT OF FREQUENCY AND DATE OF CLIPPING

The nutrient content was significantly affected by frequency and date of harvesting (Tables 11 & 12). The less frequently the plants were clipped the lower the percentage of protein, digestible organic matter, total digestible nutrients, calcium, and phosphorus, and the higher the percentage of lignin and other carbohydrates in the total harvested herbage (Fig. 7). Plants harvested at weekly, biweekly, and monthly intervals from April 15 to June 15 (treatments 5, 6, & 7) decreased in protein from 26.6% for weekly clipping to 24.0% for biweekly clipping and 19.9% for monthly clipping (Table 11).

The amount and nutrient content of the harvested herbage for each date are shown in Table 13. Protein content for herbage clipped at monthly intervals decreased from 28.2 to 18.9% from April 15 to June 15 and cellulose increased from 19.6 to 32.1%. For the same period, protein content of herbage clipped at weekly intervals decreased from 30 to 23.1% from April 15 to June 15 and cellulose increased from 19.8 to 26.2%. Lignin content and total digestible nutrients varied only slightly during this period and were not greatly different among the 3 treatments.

The weighted average percents for chemical constituents shown in Table 13 differ from those shown in Table 11. The weighted averages would be comparable to results of a single chemical analysis of the total oven dry herbage produced. Weighted averages are more informative in many respects but are not adapted to statistical interpretation by an analysis

TABLE 13. Average grams of oven-dry herbage and percent chemical content of herbage produced for 5 yrs for selected treatments clipped at various dates.

Treatment no. and chemical constituents	Clipping Dates											Total yield and weighted average composition
	4/15	4/22	5/1	5/7	5/15	5/22	6/1	6/7	6/15	7/1	10/1	
Treatment 5												
Yield	100.3	54.3	62.8	38.9	39.4	26.6	31.1	18.2	12.4		239.4	623.4
Protein	30.0	33.8	29.4	29.7	30.3	27.4	27.0	24.0	23.1		11.6	22.6
T. D. N.	71.5	73.5	69.1	71.4	70.5	68.1	69.0	66.5	62.0		63.8	67.8
Cellulose	19.8	21.6	23.7	23.1	25.4	25.1	28.1	27.2	26.2		25.9	24.2
Lignin	4.4	3.9	4.8	4.5	4.5	4.7	4.7	5.0	5.8		6.6	5.3
Treatment 6												
Yield	146.9		153.8		113.8		64.2		37.1		396.0	911.8
Protein	29.8		29.2		27.7		25.5		23.1		9.8	20.2
T. D. N.	72.6		70.6		71.0		70.8		64.7		64.5	68.1
Cellulose	18.9		22.4		25.8		28.3		27.8		26.0	24.6
Lignin	4.1		4.6		4.5		4.5		5.6		6.4	5.3
Treatment 7												
Yield	154.6				362.4				330.8		486.5	1334.3
Protein	28.2				23.1				18.9		9.7	17.7
T. D. N.	65.8				71.8				62.6		64.1	66.0
Cellulose	19.6				25.5				32.1		27.7	27.3
Lignin	4.4				4.5				6.5		6.5	5.7
Treatment 19												
Yield	161.8										2295.6	2457.4
Protein	28.9										3.6	5.2
T. D. N.	73.1										54.9	56.1
Cellulose	19.4										35.9	34.8
Lignin	4.1										8.9	8.4
Treatment 18												
Yield			391.2								1703.1	2094.3
Protein			26.1								3.3	7.5
T. D. N.			71.8								51.7	55.4
Cellulose			22.0								35.2	32.8
Lignin			4.4								9.3	8.4
Treatment 15												
Yield					687.4						1266.5	1953.9
Protein					20.0						4.4	9.9
T. D. N.					71.4						54.3	60.3
Cellulose					24.4						33.2	30.1
Lignin					4.5						13.3	10.2
Treatment 12												
Yield							1230.9				748.9	1979.8
Protein							15.7				6.4	12.2
T. D. N.							63.0				68.2	65.2
Cellulose							30.0				29.8	29.9
Lignin							6.4				5.8	6.2
Treatment 8												
Yield									1689.2		393.9	2085.1
Protein									10.9		9.1	10.5
T. D. N.									58.3		64.8	59.5
Cellulose									35.6		26.7	33.9
Lignin									7.7		6.4	7.4
Treatment 4												
Yield										2353.5	219.2	2572.7
Protein										8.2	13.6	8.6
T. D. N.										53.8	65.6	54.8
Cellulose										37.0	24.8	36.0
Lignin										8.8	6.0	8.6
Treatment 43 (control)												
Yield											2949.3	2949.3
Protein											2.8	2.8
T. D. N.											52.6	52.6
Cellulose											37.4	37.4
Lignin											9.3	9.3

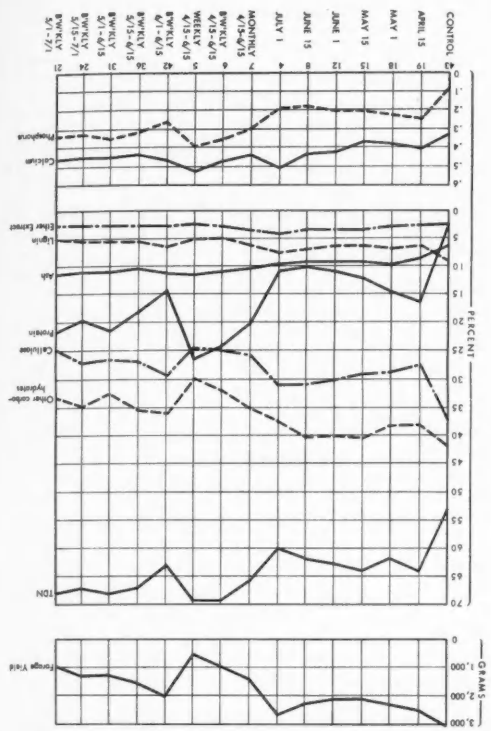

FIG. 7. Average annual forage yield per plot (10 plants) and average percent chemical content of harvested herbage over a 5-yr period for 15 selected treatments. Each sample was harvested October 1 in addition to the harvests during the growing season, and this material was included in the average chemical analysis.

of variance. For this reason, the complete analysis of data percentagewise was based on mean values derived from the sum of all single calculations from all individual samples with each determination given equal weight. This would be comparable to averaging the chemical contents of small samples of the herbage at each date without any knowledge of the total dry matter production.

The total weight produced for each chemical constituent is shown in Table 14. The weight of protein harvested was greatest for plants clipped at monthly intervals and least for the plants clipped at weekly intervals; their values were 236.7 and 151.6 gm, respectively. The comparative difference between percent content (Table 11) and weight of the protein produced (Table 14) was a result of greater herbage yield under less frequent clipping. Frequently-clipped plants maintained a high percentage of protein but yield of dry matter and, consequently, total yield of protein decreased each year throughout the experiment.

Weekly, biweekly, and monthly clippings all produced herbage relatively high in digestible protein and which would meet the requirements for lactation, growth, and maintenance of range animals throughout all clipping dates. Yield of herbage may be more important than quality of forage in comparing treatments provided palatability remains high.

A comparison of treatments clipped only once shows that with delay in clipping the percentage of protein, phosphorus, digestible organic matter, and total digestible nutrients decreased. Ether extract, lignin, cellulose, and calcium increased (Fig. 7). Content of some of the more important constituents at each harvest is shown for these 6 treatments in Table 13. The protein content varied from 28.9% for treatment 19 harvested only on April 15 to 8.2% for treatment 4 harvested only on June 15. Cellulose and lignin increased from 19 and 4 to 37 and 8.8% from April 15 to June 15, respectively. Total digestible nutrients decreased from 73.1 to 53.8%. Changes in composition of the fall-harvested herbage were opposite to this. Early-clipped plants contained high cellulose and low protein by fall. Late-clipped plants were low in cellulose and high in protein by fall.

Plants clipped at monthly, biweekly, and weekly intervals from April 15 to June 15 (treatments 7, 6, & 5) varied materially in chemical content for each date. Herbage from plants reclipped at monthly intervals (treatment 7) had 28.2, 23.0, and 18.9% protein on April 15, May 15, and June 15, respectively. Plants clipped at weekly intervals (treatment 6) had 23.0, 23.0, and 30.3% protein on April 15, May 15, and June 15, respectively (Table 13). Lignin and cellulose changed but slightly when the plants were clipped frequently. Lignin in treatments 6 and 7 was about 4.3% on April 15, 4.5% on May 15, and 6.0% on June 15. Cellulose content followed the same general trend as lignin (Table 13).

Forage from plants harvested only once during the growing season had less protein and more lignin and cellulose as date of harvesting was delayed.

Plants clipped biweekly starting May 1, May 15, and June 1 and terminating June 15 (treatments 31, 36, and 42), showed marked differences in nutrient content (Table 11). As date of initial clipping was delayed, percent protein phosphorus, digestible organic matter, and total digestible nutrients decreased. Lignin, cellulose, and other carbohydrates increased with delay of clipping and reduction in number of clippings (Table 11). The quantity of the various constituents for each of the 3 treatments (31, 36, and 42), was greater for treatments clipped fewer times with later initial clippings. In each of the 3 treatments, plants clipped at 1 in. produced a larger quantity of all nutrients than plants clipped at 3 in. and watered plants in each treatment produced a greater amount of actual nutrients than unwatered plants.

In general, it can be said that any combination of early and close clipping on unwatered plots resulted in a high quality of herbage but quantity declined rapidly each year the plants were harvested (Tables 4 & 11).

TABLE 14. Average annual weight of various constituents produced in herbage of crested wheatgrass per plot (10 plants) subjected to various clipping treatments.*

Treatment	Clipping date†	Protein	Ether extract	Lignin	Cellulose	Other carbohydrates	Ash	Calcium	Phosphorus	Digestible protein	Digestible organic matter	T. D. N.
						grams						
43	——	82.5	81.6	274.1	1116.5	1223.3	187.1	9.90	2.29	0	1496.0	1551.9
		(——)	(85.2)†	(261.1)	(1078.1)	(1170.7)	(175.0)	(8.16)	(1.77)			
19	April 15	128.5	71.3	208.1	868.8	1023.1	170.2	8.44	2.88	91.6	1516.2	1582.5
		(110.7)‡	(64.9)	(195.2)	(830.7)	(970.7)	(158.3)	(6.71)	(2.30)			
18	May 1	158.2	62.0	176.4	695.1	844.4	174.0	7.25	2.99	110.1	1246.0	1302.5
		(138.8)	(55.8)	(163.5)	(657.4)	(792.6)	(162.0)	(5.55)	(2.40)			
15	May 15	196.4	71.2	142.9	607.0	773.2	172.2	7.36	3.32	126.4	1180.0	1240.6
		(176.1)	(64.9)	(130.1)	(569.7)	(721.5)	(160.2)	(5.66)	(2.71)			
12	June 1	252.7	67.1	130.4	614.9	737.9	183.2	8.21	4.18	158.0	1191.7	1251.1
		(231.3)	(60.8)	(117.7)	(577.3)	(686.4)	(171.1)	(6.49)	(3.56)			
8	June 15	227.0	54.4	161.1	727.8	721.4	169.8	6.48	4.22	135.1	1224.8	1287.3
		(206.0)	(48.3)	(148.8)	(690.0)	(670.4)	(158.0)	(4.81)	(3.60)			
4	July 1	223.6	63.6	225.5	939.6	941.0	188.6	7.18	4.59	140.7	1461.2	1548.7
		(202.7)	(57.3)	(212.5)	(901.3)	(889.0)	(176.4)	(5.50)	(3.97)			
7	Monthly	236.7	49.8	80.1	380.3	455.4	136.4	5.71	3.52	179.3	843.0	885.7
	April 15 to June 15	(215.7)	(43.8)	(67.8)	(344.3)	(406.0)	(124.9)	(4.08)	(2.91)			
6	Bi-weekly	192.6	38.4	52.2	242.5	317.2	102.1	4.41	2.83	154.4	621.0	652.1
	April 15 to June 15	(172.6)	(33.1)	(40.7)	(208.7)	(273.3)	(91.0)	(2.89)	(2.26)			
5	Weekly	151.6	26.6	34.9	164.2	208.3	72.5	3.24	2.13	122.6	431.9	451.6
	April 15 to June 15	(132.8)	(——)	(——)	(——)	(——)	(——)	(——)	(——)			
42	Bi-weekly	239.5	68.8	124.7	600.6	712.7	191.8	7.65	4.14	162.6	1164.2	1222.1
	June 1 to June 15	(218.2)	(62.5)	(112.1)	(563.7)	(662.1)	(179.6)	(5.94)	(3.52)			
36	Bi-weekly	231.4	56.0	86.6	411.8	603.3	148.3	6.25	3.71	170.1	980.9	1026.9
	May 15 to June 15	(210.3)	(49.9)	(74.2)	(375.3)	(553.4)	(136.7)	(4.60)	(3.10)			
31	Bi-weekly	220.3	45.9	66.5	306.8	409.9	124.8	5.40	3.31	172.0	756.4	790.3
	May 15 to June 15	(199.5)	(40.0)	(54.4)	(270.7)	(362.1)	(113.5)	(3.79)	(2.71)			
24	Bi-weekly	204.9	45.7	62.4	291.9	452.3	124.8	5.23	3.14	154.3	766.9	805.4
	May 1 to June 15	(194.3)	(39.9)	(50.5)	(257.0)	(403.6)	(113.5)	(3.65)	(2.55)			
21	Bi-weekly	187.5	38.8	47.3	223.4	338.7	101.3	4.36	2.65	146.2	591.8	621.9
	May 1 to July 1	(167.7)	(33.2)	(36.4)	(191.3)	(292.5)	(90.5)	(2.91)	(2.10)			
Unwatered	1 inch height	190.0	51.6	121.6	532.7	635.0	142.6	5.6	3.0	141.1	1028.0	1078.0
	3 inch height	(191.0)	(54.7)	(123.1)	(539.7)	(631.0)	(136.0)	(5.7)	(3.1)	(138.0)	(1018.9)	(1067.1)
Average		190.5	53.2	122.4	536.2	633.0	139.3	5.7	3.0	137.8	1025.1	1072.3
Watered	1 inch height	207.1	59.3	127.8	556.4	676.9	168.8	7.2	3.6	149.8	1094.0	1147.9
	3 inch height	(194.1)	(58.6)	(126.9)	(555.4)	(673.6)	(151.8)	(7.2)	(3.5)	(138.8)	(1077.2)	(1129.8)
Average		200.6	59.0	127.3	555.9	675.2	160.3	7.2	3.5	142.3	1086.6	1139.9
Average	1 inch height	198.5	55.4	124.7	544.6	655.9	155.7	6.4	3.3	141.6	1052.4	1102.0
Average	3 inch height	192.6	56.7	125.0	547.6	652.3	143.9	6.5	3.3	136.7	1048.9	1100.2

*Treatment is a combination of season and frequency.
†All plants were clipped on October 1 each year in addition to dates shown.
‡Figures in parentheses represent lower significant limit L.S.L. which is a test of significance among treatments. Any treatment mean having a lower value than the L.S.L. of any other treatment mean is significantly different from that mean at the 5 percent level (Duncan 1955).

As the date of harvesting was delayed and plants became more mature, forage became stemmy and unpalatable compared to plants clipped earlier. After June 1, both nutritiousness and palatibility of herbage decreases markedly and this might be a more important measure than dry weight yield in evaluating these treatments in terms of a grazing system.

STEM-LEAF RATIO

In the fall, plants on watered and unwatered plots had about the same stem weight to leaf weight ratio (Table 16). However, treatments 19 and 18 which were clipped only once early in the growing season and the control, treatment 43, had a higher percentage of stems on the unwatered plots. Treatments 15, 12, 8, and 4, also clipped once but later in the growing season, had a higher percentage of stems on watered plots.

Plants clipped monthly and biweekly from April 15 to June 15 (treatments 7 and 6) had a higher stem-leaf ratio in fall herbage on unwatered plots. However, plants clipped weekly from April 15 to June 15 (treatment 5) had a higher ratio on watered plots.

Generally, plants clipped late in the growing season or more frequently had a higher stem-leaf ratio on watered plots. Plants clipped early in the growing season or less frequently had a higher stem-leaf ratio on unwatered plots.

In general, plants clipped at 3 in. had a higher stem-leaf ratio in the fall than plants clipped at 1 in.; however, plants clipped once on April 15 (treatment 19), had a higher stem-leaf ratio when clipped at 1 in. Plants harvested once on June 1 and June 15 at 1 in. (treatments 12 & 8) produced a higher percentage of stemmy material on watered plots than on unwatered plots. However, when clipped at 3 in., they produced a higher percentage of stemmy material on unwatered plots.

When plants were clipped at 3 in. height on May

TABLE 15. Analysis of variance for production of various constituents by crested wheatgrass clipped at different dates and frequencies at 1- and 3-in. heights and under dry and moist conditions for a period of 5 yrs. (See Table 14)

Source	Degrees of freedom	Mean Squares							
		Total protein	Ether extract	Lignin	Cellulose	Other carbohydrates	Ash	Calcium	Phosphorus
Water (H_2O)	1	7620.48	2525.90	1845.12	28969.02	133837.45	3312.75†	170.55†	17.66†
Year x H_2O (error a)	4	4191.47	460.20	825.97	14368.22	46741.21	571.88	2.64	1.23
Treatment (tr.)	14	44777.05†	4601.32†	105433.79†	1657803.61†	167317.31†	28181.78†	63.43†	10.77†
Height (ht.)	1	2682.03†	114.70	7.05	666.05	995.55	10413.50†	.28	.11
Tr. x ht.	14	3118.91†	422.52†	2475.22†	51974.22†	32162.15†	2233.33†	4.39	1.43*
Year (yr.)	4	696864.40†	28499.66†	163838.05†	3931077.10†	72311.24†	253143.60†	764.93†	119.44†
Yr. x tr.	56	68877.98†	434.50†	3935.06†	60697.40†	43980.37†	2273.97†	6.76	2.51†
Yr. x ht.	4	3077.66†	84.47	266.21	5741.28	5853.75	1859.16†	3.46	1.64
Yr. x tr. x ht.	56	870.37	100.83	390.96	4704.71*	11245.75†	450.54*	1.69	.78
Yr. x tr. x H_2O	56	662.11	114.85*	245.12	4662.45*	9892.67†	397.20	2.02	.62
Y_1. x ht. x H_2O	4	279.80	43.44	367.68	5576.01	10495.92	158.10	1.12	.35
Tr. x H_2O	14	3633.11†	551.98†	2697.43†	57971.48†	71946.83†	1654.65†	3.12	.77
Ht. x H_2O	1	3745.33	264.13	106.80	1212.00	5.72	2056.69†	.44	.20
Tr. x ht. x H_2O	14	1132.63	203.54*	164.37	4295.59	7330.46	706.05†	6.65	.79
Yr. x tr. x ht. x H_2O (error b)	56	790.77	71.89	298.10	2597.91	4819.48	262.94	5.28	.69

*Indicates significance at the 5% level. †Indicates significance at the 1% level.

15 (treatment 15), most of the culms in the center of the bunch were replaced from latent tiller buds. Outside culms continued to grow from the original culms. Leaves on the center culms were shorter and narrower than those on outside culms. Culms in the outside perimeter of the clump possessed many hedged leaf blades but seed heads were normal (Fig. 8). Plants clipped at 1 in. on May 15 regrew entirely from crown buds and all original culms were inactivated (Fig. 8A).

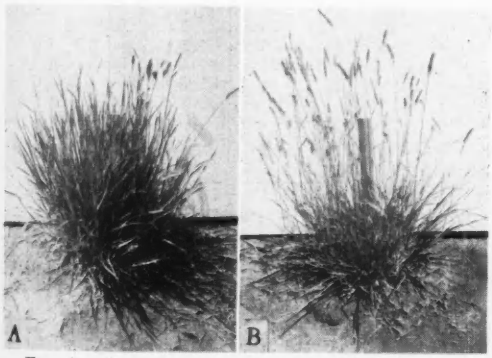

FIG. 8. General appearance of crested wheatgrass plants on July 15 following clipping (A) at 1 in. on May 15, (B) at 3 in. on May 15.

All plants clipped for the first time on May 1 to May 15 with no further harvesting produced culms that possessed only short hedged leaves. They actually appeared to be almost leafless (Fig. 9).

Unclipped plants and those clipped only once April 15 or May 1 were considerably more stemmy than plants from other treatments. The stem-leaf ratio was highest for plants clipped only on May 1 and second highest for plants clipped only on April 15. Clipping after May 15 destroyed the growing point on many culms and caused subsequent regrowth to come largely from crown buds. Plants clipped earlier were harvested above the primordia which re-

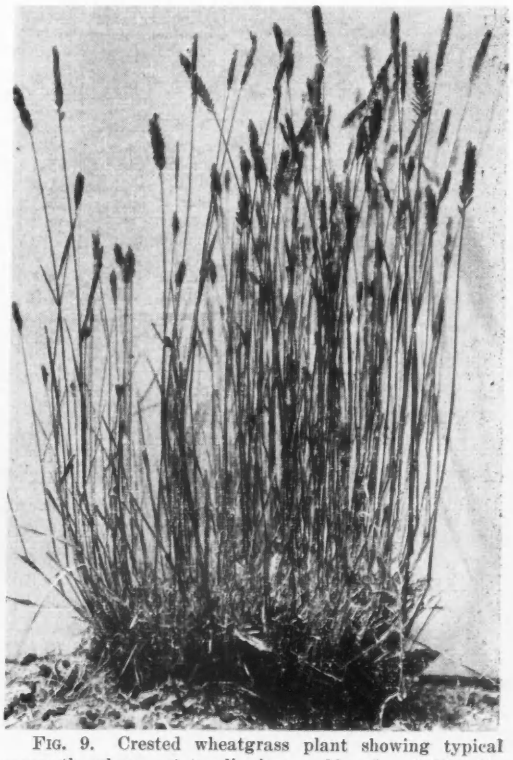

FIG. 9. Crested wheatgrass plant showing typical regrowth subsequent to clipping on May 1 and May 15. Leaves are almost absent.

TABLE 16. Chemical content and stem-leaf ratios of crested wheatgrass herbage in the fall from plants previously clipped at various dates, frequencies, and intensities.

Treatment	Clipping previous to Oct. 1	Portion of plant	Percent of total wt. of plant	Stem weight to leaf weight ratio	Protein	Ether extract	Lignin	Cellulose	Other carbohydrates	Ash	Calcium	Phosphorus
								%				
43	None	Stems	86.6		3.1	1.8	9.7	43.6	37.0	4.8	0.53	0.07
		Leaves	13.4		7.4	5.1	7.8	38.8	22.8	18.1	0.80	0.15
		Whole plant	100.0	6.46	3.7	2.2	9.4	43.0	35.1	6.6	0.57	0.08
19	April 15	Stems	89.0		3.9	2.2	9.0	40.0	40.3	4.8	0.23	0.08
		Leaves	11.0		5.6	5.5	7.9	34.9	29.6	16.4	0.90	0.08
		Whole plant	100.0	8.09	4.1	2.6	8.9	39.4	39.1	6.1	0.30	0.08
18	May 1	Stems	91.2		3.7	2.8	8.8	41.1	38.5	5.4	0.52	0.08
		Leaves	8.8		9.9	6.5	7.9	29.7	30.6	17.1	0.80	0.15
		Whole plant	100.0	10.36	4.2	3.1	8.7	40.1	37.5	6.4	0.54	0.09
15	May 15	Stems	79.2		4.3	2.4	8.4	38.4	41.9	4.6	0.27	0.09
		Leaves	20.8		7.9	7.9	7.2	31.4	30.0	15.6	0.99	0.11
		Whole plant	100.0	3.81	5.0	3.5	8.2	36.9	39.4	6.9	0.42	0.09
12	June 1	Stems	66.0		5.9	2.2	7.9	36.7	42.4	5.0	0.34	0.12
		Leaves	34.0		11.7	8.9	6.7	28.6	30.2	14.0	1.09	0.16
		Whole plant	100.0	1.94	7.9	4.5	7.5	33.9	38.3	8.1	0.60	0.13
8	June 15	Stems	57.0		6.2	2.3	7.0	34.5	44.9	4.9	0.33	0.11
		Leaves	43.0		12.0	8.4	6.0	27.1	31.9	14.6	1.18	0.16
		Whole plant	100.0	1.33	8.7	4.9	6.6	31.3	39.3	9.1	0.70	0.13
4	July 1	Stems	9.7		6.1	2.6	7.1	34.7	43.7	5.8	0.39	0.16
		Leaves	90.3		14.5	8.0	5.6	28.4	28.9	14.6	1.16	0.20
		Whole plant	100.0	0.11	13.7	7.5	5.8	29.3	30.0	13.7	0.85	0.20
7	monthly	Stems	72.4		7.5	3.6	8.4	39.4	38.4	5.2	0.25	0.08
	Apr. 15-June 15	Leaves	27.6		14.1	7.9	6.5	26.3	29.2	16.0	0.99	0.16
		Whole plant	100.0	2.62	9.3	4.8	7.9	35.8	35.9	8.2	0.45	0.10
6	biweekly	Stems	63.8		7.3	2.5	8.1	35.4	41.2	5.5	0.28	0.10
	Apr. 15-June 15	Leaves	36.2		14.7	8.3	6.3	25.4	31.2	14.1	1.05	0.18
		Whole plant	100.0	1.76	9.8	4.6	7.5	31.8	37.7	8.6	0.56	0.13
5	weekly	Stems	49.0		9.8	4.8	8.0	37.4	34.4	5.6	0.34	0.13
	Apr. 15-June 15	Leaves	51.0		15.9	8.6	6.3	25.3	29.5	14.4	0.98	0.17
		Whole plant	100.0	0.96	12.9	6.7	7.1	31.2	31.9	10.0	0.66	0.15
42	biweekly	Stems	69.8		4.4	2.7	7.6	36.2	44.7	4.4	0.25	0.11
	June 1-June 15	Leaves	30.2		8.3	8.7	6.3	29.9	32.2	14.5	1.21	0.13
		Whole plant	100.0	2.31	5.6	4.5	7.2	33.3	40.4	7.5	0.54	0.12
36	biweekly	Stems	78.9		4.8	2.7	8.1	39.1	40.6	4.7	0.35	0.10
	May 15-June 15	Leaves	21.1		9.6	8.8	6.4	28.4	31.0	15.7	1.21	0.13
		Whole plant	100.0	3.74	5.8	4.0	7.7	36.8	38.6	7.0	0.53	0.11
31	biweekly	Stems	64.4		8.6	3.2	8.2	35.4	39.4	5.1	0.30	0.13
	May 1-June 15	Leaves	35.6		12.1	8.1	7.1	26.2	31.7	14.8	1.22	0.18
		Whole plant	100.0	1.81	9.8	4.9	7.8	32.1	36.7	8.6	0.62	0.15
Unwatered		Stems	67.6		5.4	3.2	8.7	37.1	40.4	5.2	0.32	0.10
		Leaves	32.4		10.0	8.1	7.3	30.1	29.4	15.1	1.02	0.15
		Whole plant	100.0	2.09	6.9	4.8	8.2	34.8	36.9	8.4	0.55	0.12
Watered		Stems	67.7		5.8	2.4	8.6	38.1	39.0	5.5	0.32	0.11
		Leaves	32.3		11.9	7.4	6.9	28.9	29.2	15.7	1.11	0.16
		Whole plant	100.0	2.10	7.8	4.0	7.1	35.5	36.8	8.8	0.58	0.13
1 inch		Stems	63.5		6.2	2.6	8.6	38.1	38.9	5.6	0.29	0.11
		Leaves	36.5		11.8	6.9	6.8	29.1	30.3	15.1	1.02	0.16
		Whole plant	100.0	1.74	8.2	4.1	7.9	34.8	35.9	9.1	0.55	0.13
3 inch		Stems	71.4		5.0	2.9	8.8	37.7	40.4	5.2	0.35	0.10
		Leaves	28.6		10.1	8.6	7.3	29.4	29.0	15.6	1.10	0.14
		Whole plant	100.0	2.50	6.4	4.5	8.4	35.3	37.3	8.1	0.56	0.11

sulted in continued elongation of the initial culms. Regrowth from crown buds possessed few cropped leaves, whereas continued growth from the original culms possessed almost no lower leaves and only cropped leaves on the upper nodes (see also Cook & Stoddart 1953).

A single clipping late in the growing season (treatment 4) or frequent harvesting throughout the season (treatment 5) produced the smallest stem-leaf ratios. Here regrowth was entirely from tiller buds.

Frequency of clipping had a profound influence on stem-leaf ratio. Plants clipped monthly (treatment 7) had 72.4% stems compared to plants clipped biweekly and weekly (treatments 6 & 5) which had 63.8 and 49.0% (Table 16). Frequent clipping resulted in less vigorous growth which was more leafy. This was a result of frequent clipping producing more vegetative growth and fewer seed culms.

NUTRIENT CONTENT OF FALL HERBAGE

Differences in chemistry of herbage in the fall were largely a result of stem-leaf ratio. Leaves were

higher in percent protein, ether extract, ash, calcium, and phosphorus. Stems were higher in lignin, cellulose, and other carbohydrates. Also, the chemical composition of both stems and leaves harvested in the fall differed materially among the various treatments. Thus, the two factors, changes in stem-leaf ratio and changes in the chemical content of plant tissue, combined to make the chemistry of the plant doubly variable among treatments.

In general, fall herbage from watered plots was higher in percent protein, cellulose, ash, calcium, and phosphorus in both leaves and stems. Herbage from unwatered plots was higher only in ether extract and lignin. There was little difference in the percent of other carbohydrates (Table 16).

In most cases, both stems and leaves of plants clipped at 1 in. were higher in percent protein and phosphorus in the fall, whereas 3-in. plants were higher in ether extract and lignin (Table 16).

The effect of intensity of clipping on chemical content of forage harvested in the fall varied widely. For example, both stems and leaves from plants harvested only on May 15 (treatment 15) had higher percentages of phosphorus, protein, and ether extract, and somewhat less lignin when harvested at 3 in. than when harvested at 1 in. These differences were most pronounced on unwatered plots.

Delay in clipping date of once-clipped plants (treatments 19, 18, 15, 12, 8, & 4 of Table 16) resulted in higher percentages of protein, ether extract, ash, calcium, and phosphorus in both stems and leaves of autumn herbage and also reduced the stem-leaf ratio. Percentages of cellulose and lignin were decreased by delayed clipping. Percent of other carbohydrates showed no definite trend except that plants not harvested until July 1 (treatment 4) produced subsequent growth that was leafy, and decidedly low in other carbohydrates.

Plants clipped at weekly intervals had a higher percentage of leafy material than plants clipped at biweekly or monthly intervals. Consequently, plants clipped weekly (treatment 5) had higher percentages of protein, ether extract, ash, calcium, and phosphorus, and lower percentages of lignin, cellulose, and other carbohydrates than plants clipped monthly (treatment 7). Biweekly clipping (treatment 6) usually gave intermediate results.

QUANTITY OF ROOTS

Data on quantity of roots produced under the various treatments are shown in Tables 17 & 18.

EFFECT OF WATER

Plants receiving additional water produced an average of 112.55 gm of roots, whereas unwatered plants produced 118.45 gm.

An interesting interaction occurred between the application of water and clipping height (Table 18). Plants clipped at 1 in. produced slightly greater average weight of roots when watered, whereas plants clipped at 3 in. produced a greater weight of roots when unwatered.

EFFECT OF CLIPPING HEIGHT

Height of clipping had a significant effect upon root growth (Fig. 10). The average yield for the 1-in. height was 107.67 gm and for the 3-in. height 123.33 gm (Table 17). However, plants clipped at 1-in. height in treatments 7, 15, 18, and 36 produced a greater root yield than plants clipped at 3 in.

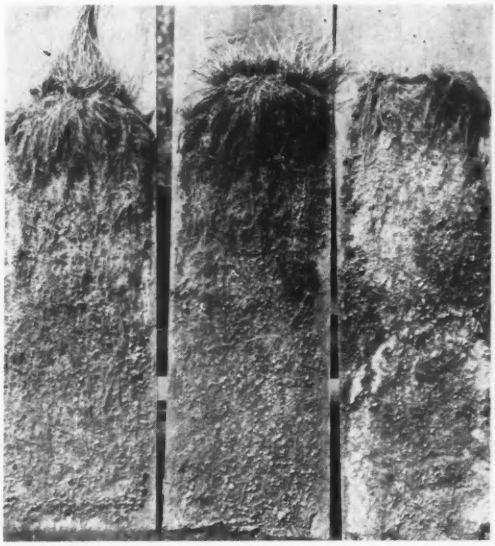

FIG. 10. Crested wheatgrass roots excavated to a depth of 4 ft. The plants were from watered plots and are left to right (a) the control, (b) clipped monthly from April 15 to June 15 at 3 in. and (c) clipped monthly April 15 to June 15 at 1 in. Significantly fewer roots were found on the clipped plants than on the control and there were significantly fewer roots with closer clipping.

Reduction in average total weight of roots because of closer clipping occurred in all three soil depths; however, the reductions because of height of clipping were more pronounced in the 0 to 6 in. depth than in the 6 to 12 or the 12 to 18 in. depths (Table 17).

In general, the data indicate that when plants were clipped at biweekly intervals until late in the growing season, neither height of clipping, nor additional water had any significant influence upon root yield.

EFFECT OF FREQUENCY AND DATE OF CLIPPING

There were highly significant differences in root yields among treatments. Unclipped plants and those clipped fewest times and earliest in the season produced the greatest root yield. When the plants were clipped only once during the growing season, the root yield was reduced as the date of clipping was delayed (treatments 19, 18, 15, 12, 8, & 4). Late season harvesting apparently leaves little time for herbage replacement before summer dormancy; hence food manufacture is limited and root growth retarded. This

TABLE 17. Average air-dry weight of roots in a column of soil 12 in. square and 18 in. deep from crested wheatgrass plants when clipped at 2 heights and at various seasons and frequencies on both watered and unwatered plots for a period of 5 yrs. Also shown are average number of roots counted in bisect below crown, depth of zone of root concentration, maximum depth of root penetration, and number of main roots approaching maximum depths.

Treatment number	Dates clipped*	Root Weights, gms.				Roots emerging from crown	Depth of zone of root concentration	Maximum depth of root penetration	No. of main roots approaching maximum penetration‡
		0 to 6	6 to 12	12 to 18	Total				
						(number)	(inches)		(number)
43	Control	216.38	13.11	12.00	241.49	164	20	6′ 2″	4.2
		(186.68)†	(10.93)	(9.78)	(219.83)	(138)†	(18)	(5′ 9″)	(2.7)
19	April 15	165.70	11.99	9.67	187.37	178	17	6′ 6″	5.0
		(136.13)	(9.81)	(7.46)	(165.80)	(152)	(15)	(6′ 1″)	(3.5)
18	May 1	152.11	8.27	6.13	166.51	129	17	4′ 10″	4.8
		(122.67)	(6.11)	(3.93)	(145.04)	(104)	(15)	(4′ 6″)	(3.3)
15	May 15	137.98	9.44	5.65	153.07	132	14	4′ 9″	2.8
		(108.67)	(7.27)	(3.47)	(131.71)	(107)	(12)	(4′ 6″)	(—)
12	June 1	116.49	8.20	5.78	130.47	138	14	5′ 6″	4.5
		(87.48)	(6.05)	(3.59)	(109.26)	(113)	(12)	(5′ 1″)	(3.0)
8	June 15	103.36	6.58	3.25	113.19	154	15	5′ 4″	2.5
		(74.52)	(4.47)	(1.11)	(92.49)	(128)	(13)	(4′ 11″)	(—)
4	July 1	102.02	7.78	4.09	113.89	119	16	4′ 6″	3.0
		(73.36)	(5.65)	(1.94)	(92.49)	(95)	(14)	)	(—)
7	Monthly	81.05	4.59	2.10	87.74	123	14	4′ 9″	4.2
	April 15-June 15	(52.99)	(2.53)	(——)	(67.46)	(98)	(12)	(4′ 6″)	(2.8)
6	Bi-weekly	69.42	3.20	1.44	74.06	98	14	5′ 10″	3.8
	April 15-June 15	(——)	(——)	(——)	(——)	(76)	(12)	(5′ 5″)	(2.4)
5	Weekly	54.89	3.65	1.47	60.01	74	9	5′ 0″	2.8
	April 15-June 15	(——)	(——)	(——)	(——)	(—)	(—)	(4′ 8″)	(—)
42	Bi-weekly	117.61	7.58	4.82	130.01	130	18	5′ 6″	5.5
	June 1-June 15	(88.43)	(5.46)	(2.65)	(108.95)	(105)	(16)	(5′ 1″)	(4.0)
36	Bi-weekly	100.58	5.34	2.73	108.65	114	16	5′ 8″	3.2
	May 15-June 15	(72.18)	(3.25)	(——)	(88.13)	(90)	(14)	(5′ 3″)	(—)
31	Bi-weekly	72.21	4.18	1.75	78.14	104	14	5′ 4″	3.0
	May 1-June 15	(——)	(——)	(——)	(58.13)	(81)	(12)	(5′ 0″)	(—)
24	Bi-weekly	70.67	4.13	1.85	76.65	97	11	4′ 5″	2.2
	May 15-July 1	(——)	(——)	(——)	(57.03)	(76)	(9)	(——)	(—)
10	Bi-weekly	64.58	4.58	2.10	71.26	100	17	5′ 2″	3.0
	April 15-June 1	(——)	(2.54)	(——)	(——)	(77)	(15)	(4′ 10″)	(—)
21	Bi-weekly	52.12	2.47	1.00	55.59	110	15	5′ 5″	4.5
	May 1-July 1	(——)	(——)	(——)	(——)	(86)	(13)	(5′ 0″)	(3.0)
Unwatered	1 inch height	96.45	6.49	3.86	106.80	115	13	5′ 2″	2.9
	3 inch height	118.30	7.40	4.42	130.12	113	15	5′ 4″	3.3
Average		107.37	6.94	4.14	118.45	114	14	5′ 3″	3.1
Watered	1 inch height	98.76	6.14	3.66	108.56	127	15	5′ 0″	4.2
	3 inch height	105.79	6.24	4.53	116.56	137	15	5′ 8″	3.8
Average		102.27	6.19	4.09	112.55	132	15	5′ 4″	4.0
Average	1 inch height	97.60	6.31	3.76	107.67	121	14	5′ 1″	3.6
	3 inch height	112.04	6.82	4.47	123.33	125	15	5′ 6″	3.6

*All plants were clipped on October 1 in addition to dates shown.
†Figures in parenthesis represent the lower significant limit (L.S.L.) which is a measure of significance among means. Any treatment mean having a lower value than the L.S.L. of another treatment mean is significantly lower than that mean at the 5% level (Duncan 1955).
‡This includes all roots reaching a depth within 4in. of the deepest root measured.

agrees with findings of Smith & Graber (1948) who showed that later harvesting reduced yield of roots more than earlier harvesting.

Plants clipped at monthly intervals from April 15 to June 15 produced an average of 87.74 gm of roots compared to 60.1 gm from plants clipped at weekly intervals for the same period (Table 17). These yields were significantly lower than any treatments where the plants were clipped only once during the growing season. This agrees with the findings of Weinmann (1943, 1944) and Lovvorn (1945) who showed that increased frequency of clipping grasses significantly reduced root yield.

Plants clipped 2, 3, and 4 times, commencing June 1, May 15, and May 1, respectively, but ending on June 15 (treatments 42, 36, 31) showed progressive decreases in root yield.

Frequency of clipping and date of herbage removal both had greatest effect upon root yield in the upper 6 in. of soil (Table 17, 18).

Number of Roots and Root Penetration

Data for average number of roots, depth of root

TABLE 18. Analysis of variance for crested wheatgrass root weight data presented in table 17.

Source	Degrees of freedom	Mean squares
Water (H_2O)	1	370.48
Replication (rep.)	1	741.93
Error (a) (rep. x H_2O)	1	588.36
Depth	2	422,454.66†
Error (b) (rep. x depth)	2	1,067.38†
Depth x H_2O	2	239.72
Treatment (tr.)	15	7,032.75†
Height (ht.)	1	2,577.03†
Tr. x H_2O	15	177.11
Tr. x depth	30	4,763.15†
Tr. x ht.	15	360.87†
Ht. x H_2O	1	666.48*
Ht. x depth	2	2,060.63†
H_2O x tr. x ht.	15	132.13
H_2O x tr. x depth	30	148.40
Ht. x H_2O x depth	2	548.00†
Ht. x tr. x depth	30	343.71†
Ht. x tr. x depth x H_2O	30	710.55†
Error (c)	188	107.72

*Denotes significance at the 5% level.
†Denotes significance at the 1% level.

concentration, and maximum root penetration are presented in Tables 17 and 19.

EFFECT OF WATER

Plants in watered plots produced a significantly greater number of roots (aver. 132) than unwatered plants (aver. 114) and had a concentration of roots down to 15 in. compared to 14 in. for unwatered plants. The average unwatered plant clipped at 1 in. had a concentration of roots in the top 13 in. of soil compared to 15 in. for plants clipped at 3 in. The average watered plant had a concentration of roots down to 15 in. regardless of clipping height.

TABLE 19. Analysis of variance for roots produced below crown, depth of zone of root concentration, maximum depth of root concentration, and number of main roots approaching maximum depths for various treatments clipped at 1- and 3-in. height on watered and unwatered plots for data presented in table 17.

Source	Degrees of freedom	Mean Squares: Number of roots emerging from crown	Depth of zone of root concentration	Maximum depth of root penetration	No. of main roots approaching max. penetration
Treatment (tr.)	15	8,793.59†	80.41†	4.19†	13.42†
Height (ht.)	1	652.08	26.26†	4.84†	.88
Water (H_2O)	1	15,624.08†	34.17†	.01	49.01†
Tr. x ht.	15	1,425.82*	8.21*	3.55†	18.96†
Tr. x H_2O	15	624.79	12.53†	2.93†	14.08†
Ht. x H_2O	1	1,633.34	49.00†	1.36†	7.92
Tr. x ht. x H_2O	15	1,515.93†	13.34†	1.60†	6.98
Error	128	685.35	3.80	.14	2.80

*Denotes significance at 5% level.
†Denotes significance at 1% level.

There was no significant difference in maximum depth of roots on watered and unwatered plots, but watered plants had an average of 4 roots approaching maximum depth, whereas unwatered plants had only 3.1. Roots in some treatments had greater penetration on watered plots, but in many of the same treatments, number of roots approaching maximum penetration was greater on unwatered plots.

EFFECT OF CLIPPING HEIGHT

Height of clipping had a significant effect upon depth of root concentration and maximum depth of penetration, but did not significantly influence the number of roots per plant or number of roots approaching maximum penetration.

In general, plants clipped at 1 in. did not produce roots as deep as plants clipped at 3 in. This difference was more pronounced on watered plots than on unwatered plots (Table 17).

EFFECT OF FREQUENCY AND DATE OF CLIPPING

Date and frequency of clipping had significant effects on both number and depth of roots. When plants were clipped only once during the growing season, early clipping (April 15) did not decrease number or depth of roots compared to unclipped control plants (Table 17). However, late clipping (July 1) reduced both the number and depth of roots. Each delay in date of clipping between April 15 and July 1 materially reduced the number of roots on unwatered plants. Among watered plants such reduction in number of roots was evident only when clipped late in the season. These reductions in number of roots were greater for plants clipped at 1 in. than for those clipped at 3 in.

In general, each delay in date of clipping between April 15 and July 1 reduced depth of root concentration, maximum depth of penetration, and number of roots approaching maximum depth (Table 17).

Treatments 7, 6, and 5 clipped at monthly, biweekly, and weekly intervals from April 15 to June 15, produced significant differences in number and depth of roots (Tables 17, 19). Plants clipped weekly averaged 74 roots per plant, whereas plants clipped monthly averaged 123 roots. Differences were greatest for unwatered plants and 1-in. clipping heights. The frequently-clipped plants also had shallower root concentration and penetration.

Generally, number of roots per plant correlated with weight of roots. In some cases, however, roots were numerous but small or they were few but large. Leukel (1927) and Wagner (1952) found that clipped plants produced a greater number of roots of smaller sizes than unclipped plants. In the present study almost any combination of clipping reduced root numbers as well as depth. This is important since, with decreased root number and depth, the volume of soil from which moisture and nutrients can be absorbed is decreased. This limits the capacity of plants to acquire moisture and nutrients.

CHEMICAL CONTENT OF ROOTS

Little is known about how storage and utilization of food reserves are affected by periodic harvesting of

TABLE 20. Average percent chemical composition of crested wheatgrass roots for various treatments* clipped at 1-and 3-in. heights on watered and unwatered plots. These figures are unweighted averages of the composition of roots from the 0- to 6-in., 6- to 12-in., and 12- to 18-in. depths.

Treatment number	Dates clipped†	Ether extract	Protein	Ash	Calcium	Phosphorus	Lignin	Cellulose	Other carbohydrates	Reducing sugar	Sucrose	Fructosan	Hemicellulose
43	Control	.53	5.53	31.8	3.13	.144	13.5	18.1	30.6	3.34	.75	4.95	17.9
		(—)‡	(—)	(—)	(2.58)	(—)	(—)	(—)	(—)	(3.08)	(.70)	(4.47)	(—)
19	April 15	.53	5.49	32.9	3.42	.147	13.5	17.8	29.8	2.89	.64	4.12	17.1
		(—)	(—)	(—)	(2.86)	(—)	(—)	(—)	(—)	(2.63)	(.59)	(3.64)	(—)
18	May 1	.62	5.81	31.2	3.04	.149	14.4	19.1	28.9	2.15	.54	3.70	17.6
		(.52)	(—)	(—)	(2.50)	(—)	(—)	(—)	(—)	(1.89)	(.49)	(3.23)	(—)
15	May 15	.63	5.75	32.8	2.96	.152	14.6	19.1	27.2	1.63	.44	2.73	16.9
		(.53)	(—)	(—)	(2.42)	(—)	(13.5)	(—)	(—)	(1.38)	(.39)	(2.26)	(—)
12	June 1	.59	5.83	33.7	3.31	.144	14.2	19.0	26.8	1.47	.34	2.37	17.9
		(.49)	(—)	(—)	(2.76)	(—)	(—)	(—)	(—)	(1.22)	(.29)	(1.90)	(—)
8	June 15	.58	6.08	26.9	2.58	.140	16.4	21.5	28.5	1.16	.23	1.91	18.6
		(.49)	(5.70)	(—)	(—)	(—)	(15.3)	(19.2)	(—)	(.92)	(.18)	(1.48)	(—)
4	July 1	.53	5.76	31.1	2.76	.136	15.2	19.8	27.8	1.30	.32	2.13	17.9
		(—)	(—)	(—)	(—)	(—)	(14.1)	(—)	(—)	(1.05)	(.27)	(1.67)	(—)
7	Monthly	.54	6.73	27.2	2.43	.152	16.5	21.3	27.9	1.07	.20	2.01	18.4
	April 15-June 15	(.45)	(6.34)	(—)	(—)	(—)	(15.3)	(19.1)	(—)	(.83)	(.15)	(1.56)	(—)
6	Bi-weekly	.57	7.12	25.2	2.32	.148	17.2	21.5	28.5	.94	.13	1.81	19.4
	April 15-June 15	(.48)	(6.72)	(—)	(—)	(—)	(16.0)	(19.3)	(—)	(.71)	(—)	(—)	(—)
5	Weekly	.56	7.16	27.9	2.67	.147	17.0	20.3	27.1	.78	.13	1.39	18.7
	April 15-June 15	(.47)	(6.76)	(—)	(—)	(—)	(15.8)	(18.1)	(—)	(—)	(—)	(—)	(—)
42	Bi-weekly	.54	5.95	29.6	3.28	.150	15.2	19.4	29.4	1.86	.58	2.31	17.8
	June 1-June 15	(.45)	(5.57)	(—)	(2.73)	(—)	(14.1)	(—)	(—)	(1.60)	(.53)	(1.85)	(—)
36	Bi-weekly	.55	6.55	26.1	2.58	.147	17.0	21.3	28.5	1.31	.43	2.06	18.6
	May 15-June 15	(.46)	(6.16)	(—)	(—)	(—)	(15.8)	(19.1)	(—)	(1.06)	(.38)	(1.60)	(—)
31	Bi-weekly	.63	7.23	25.0	2.25	.153	18.0	22.3	27.0	1.23	.22	1.98	18.4
	May 1-June 15	(.53)	(6.82)	(—)	(—)	(—)	(16.8)	(20.0)	(—)	(.98)	(.17)	(1.54)	(—)
24	Bi-weekly	.61	6.80	27.2	2.62	.148	17.2	21.7	26.6	.98	.15	1.73	18.8
	May 15-July 1	(.51)	(6.41)	(—)	(—)	(—)	(16.0)	(19.4)	(—)	(.75)	(—)	(—)	(—)
10	Bi-weekly	.43	6.84	28.3	2.72	.148	16.3	21.0	27.2	.85	.13	2.00	18.8
	April 15-June 1	(—)	(6.44)	(—)	(—)	(—)	(15.2)	(18.8)	(—)	(—)	(—)	(1.55)	(—)
21	Bi-weekly		7.18	23.5	2.32	.153	18.4	23.0	27.3	.70	.14	1.76	18.8
	May 1-July 1	(—)	(6.78)	(—)	(—)	(—)	(—)	(20.7)	(—)	(—)	(—)	(—)	(—)
Unwatered	1 inch height	.64	6.65	29.4	2.73	.143	15.8	20.2	27.4	1.44	.31	2.21	18.2
	3 inch height	.49	6.31	30.8	2.86	.144	15.7	19.4	27.3	1.41	.33	2.53	17.8
Average		.56	6.48	30.1	2.80	.144	15.8	19.8	27.4	1.42	.32	2.37	18.0
Watered	1 inch height	.58	6.38	27.7	2.75	.153	15.8	20.7	28.9	1.45	.32	2.34	18.5
	3 inch height	.56	6.12	27.2	2.75	.150	16.3	21.3	28.6	1.62	.38	2.65	18.5
Average		.57	6.25	27.4	2.75	.152	16.0	21.0	28.8	1.54	.35	2.50	18.5
Average	1 inch height	.61	6.51	28.5	2.74	.148	15.8	20.4	28.1	1.45	.32	2.28	18.3
	3 inch height	.53	6.21	29.0	2.81	.147	16.0	20.3	28.0	1.52	.35	2.59	18.1
	0-6″ depth	0.75	7.16	32.17	2.34	0.15	15.93	15.94	28.18	1.12	0.23	1.85	17.50
	6-12″ depth	0.46	6.41	28.50	2.39	0.16	15.96	21.45	27.22	1.44	0.33	2.36	18.29
	12-18″ depth	0.49	5.52	25.68	3.58	0.13	15.80	23.76	28.75	1.88	0.44	3.09	18.92

*Treatment is a combination of season and frequency of clipping.
†All plants were clipped on October 1 in addition to dates shown.
‡Figures in parentheses represent lower significant limits (L.S.L.) which serve as a test of significance among means. Any treatment mean of a lower value than the L.S.L. of a higher treatment mean, is significantly lower from that mean at the 5% level (Duncan 1955).

herbage. It is not clearly understood which organic materials constitute food reserves, although it is generally agreed that the more soluble forms of carbohydrates are most important.

Some research has indicated that once cellulose, hemicellulose, and lignin are laid down in the cell wall, they cannot be remobilized (Bonner 1950, Norman & Richardson 1937, Sullivan & Sprague 1943, Weinmann 1948a, 1952). However, Arny (1932) and Buston (1935 obtained data which indicated that some forms of hemicellulose could be used as reserves when less soluble carbohydrates were not available. Weinmann, (1952) found that hemicellulose and pentosan in roots of grasses varied inversely with the content of soluble carbohydrates.

Meyer & Anderson (1952) and Bonner (1950) stated that fats and fat-like substances can serve as stored food in plants and sometimes play a significant role in this capacity. However, Weinmann (1949) concluded that fats in roots of grasses did not serve as reserve food since percent fat content showed no relation to intensity of herbage removal.

McCarty (1935, 1938) and Sampson & McCarty (1930) have shown that maximum storage of food reserves in the roots of grasses is attained after the current growth approaches maturity. If herbage is removed during the growing season, the plant depletes its reserves in regrowth and full storage potential is never reached.

Chemical content of root material is generally presented on a percentage basis but changes percentagewise for a given constituent may result from

TABLE 21. Analysis of variance for percent of chemical constituents in crested wheatgrass roots from a cube of soil 1 ft by 1 ft at 3 depths for various clipping treatments on watered and unwatered plots for data presented in table 21. Roots from the 2 replications were composited for chemical analysis.

Source	Degrees of freedom	Ether extract	Protein	Ash	Calcium	Phosphorus	Lignin	Cellulose	Other carbohydrates	Reducing sugar	Sucrose	Fructusan	Hemicellulose
Water (H_2O)	1	.0005	2.61†	329.96*	.10	.0034†	4.32	66.04†	89.24*	.51	.033†	.748	14.52
Treatment (tr.)	15	.037*	5.00†	119.57	1.69†	.0002	28.86†	28.18†	16.51	6.81†	.504†	11.512†	5.37
Height (ht.)	1	.31	4.32†	11.07	.20	.0001	1.73	.56	1.49	.23	.057†	4.551	1.96
Tr. x ht.	15	.025	.18	2.86	.30	.0001	1.32	4.64	7.56	.28	.004	.840	2.99
Tr. x H_2O	15	.015	.18	23.29	.22	.0002	1.18	5.21	5.58	.20	.006	.476	2.06
Ht. x H_2O	1	.22	.09	45.15	.16	.0003	3.15	23.80*	.43	.50	.017*	.001	1.96
Ht. x tr. x H_2O (a)	15	.015	.13	52.45	.48	.0001	2.49	4.80	13.49	.35	.003	1.330	5.37
Depth	2	1.64†	43.50†	677.65	31.47†	.0104*	.48	32.54*	37.98	9.34	.744†	24.548*	32.41*
Depth x H_2O (b)	2	.01	.28	103.13*	.26	.0002	1.51	41.56†	29.68†	.52†	.007	.623	.65
Depth x tr.	30	.01	.24	78.22†	1.35†	.0001	3.24	21.08†	18.88†	.75†	.026†	1.698†	3.66
Depth x ht.	2	.01	.33	14.08	.47	.0002	4.13	39.40†	15.31	.32*	.012*	1.206†	.11
Depth x tr. x ht.	30	.01	.24	28.47	.30	.0001	1.34	3.75	7.14	.08	.006*	.335	2.62
Error (c)	62	.01	.17	23.52	.32	.0001	1.47	5.38	7.78	.07	.003	.234	2.60

*Denotes significance at the 5% level. †Denotes significance at the 1% level.

change in some other constituent. Therefore, in this study, changes in both percent and actual amount are presented in discussing effects of herbage removal on the chemistry of the root. Roots were excavated from the 0- to 6-in. depth (including crowns), the 6- to 12-in. depth, and the 12- to 18-in. depth. Material from each depth was weighed and analyzed separately. Percentage figures (Table 20) are unweighted averages of the chemical content at the three depths. Table 22 shows the total weight of each constituent produced in the 3 depths combined when treatment averages are multiplied by 3.

In the conventional proximate analysis, carbohydrates other than cellulose and lignin are grouped as an analytical fraction called *other carbohydrates*. The percent of other carbohydrates is found by subtracting percent ether extract, protein, ash, cellulose, and lignin from 100%. A more detailed analysis would include reducing sugar, sucrose, fructosan, starch, and hemicellulose rather than other carbohydrates. In this study, the total of the other carbohydrates fraction by actual analysis was somewhat less than the total for other carbohydrates as determined by difference. This discrepancy may be accounted for by the presence of other minor compounds for which separate determinations were not made. Such compounds would include organic acids, pectic compounds, pigments, gums, mucilages, and alkaloids. Starch was not present in the root samples analyzed and therefore does not constitute any portion of the carbohydrate fraction.

EFFECT OF WATER

Roots from plants receiving additional water had significantly higher average percentages of phosphorus, cellulose, sucrose, and other carbohydrates. Roots from drier plants had significantly higher percentages of protein and ash (Table 20). Watered plants produced more foliage; therefore they may have demanded more nitrogen from the roots, thereby lowering the protein percentage present in the roots. Additional soil moisture no doubt makes phosphorus more available for absorption and results in increased content in the roots as well as the foliage. Both percentage and total weight of reducing sugars, sucrose, and fructosan were increased somewhat by additional water. Greater photosynthetic activity in watered plants may account for higher sugar content compared to unwatered plants.

There was little difference in percent of cellulose or sucrose between roots from watered and unwatered plants when clipped at 1 in. height but both were considerably higher in roots from watered plants when clipped at 3 in. (Tables 20, 21). This failure of water to increase root carbohydrates in plants clipped at 1 in. may have resulted from decreased photosynthetic tissue and delayed growth resulting from close clipping. Cellulose in roots at depths of 12 to 18 in. was greater on watered plots than on unwatered plots, whereas there was no difference at shallower depths between watered and unwatered plots.

Despite the slightly greater average yield of roots on unwatered plants there was a greater weight of phosphorus, cellulose, reducing sugars, and fructosan produced in roots of watered plants.

The other carbohydrates in roots of unwatered plants averaged 27.4%, whereas roots of watered plants contained 28.8% (Table 21). The influence of water on these carbohydrates was not the same at all soil depths. On unwatered plots the percent increased with increased depth of roots. On watered plots it decreased.

Water also had a differential effect on percent of reducing sugars at different depths. On unwatered plots the roots contained about the same percent at all depths; but on watered plots the percent increased with increased depth.

The percent of fructosan tended to be higher in roots from watered plots than unwatered but differences were not significant.

These data on effect of water upon carbohydrate content of roots agree with findings of Smith (1950) in which he reported that percent of available carbohydrates in the roots was reduced during dry periods

TABLE 22. Average production of various constituents in the roots of crested wheatgrass in grams from a column of soil 1 ft by 1 ft and 18 in. deep* for various treatments clipped at 1- and 3-in. stubble height and from watered and unwatered plots.

Treatment number	Dates clipped†	Ether extract	Protein	Ash	Calcium	Phosphorus	Lignin	Cellulose	Other carbohydrates	Reducing sugar	Sucrose	Fructosan	Hemicellulose
43	Control	.53	4.97	28.2	2.02	.121	11.2	12.3	23.4	1.56	.485	2.25	13.4
		(.43)‡	(4.40)	(23.4)	(1.68)	(.107)	(10.0)	(10.9)	(20.4)	(1.34)	(.452)	(1.97)	(11.9)
19	April 15	.42	3.70	21.5	1.71	.095	8.6	10.0	18.4	1.19	.318	1.68	10.4
		(.32)	(3.13)	(16.7)	(1.37)	(.081)	(7.4)	(8.6)	(15.4)	(.97)	(.285)	(1.40)	(8.9)
18	May 1	.43	3.47	19.8	1.45	.084	7.9	8.1	15.8	.87	.202	1.29	9.4
		(.33)	(2.90)	(15.0)	(1.11)	(.070)	(6.7)	(6.7)	(12.8)	(.65)	(.170)	(1.01)	(8.0)
15	May 15	.42	3.26	17.8	1.20	.080	7.6	8.0	14.0	.66	.155	1.14	8.6
		(.32)	(2.70)	(13.0)	(.86)	(.066)	(6.4)	(6.6)	(11.0)	(.44)	(.123)	(.87)	(7.2)
12	June 1	.35	2.86	13.3	1.01	.062	6.7	7.9	12.4	.60	.082	.95	7.8
		(.25)	(2.30)	(8.6)	(.68)	(.048)	(5.5)	(6.5)	(9.5)	(.39)	(.051)	(.68)	(6.4)
8	June 15	.28	2.48	10.7	.80	.057	6.1	6.7	11.4	.40	.060	.71	6.9
		(.19)	(1.93)	(6.1)	(.48)	(.044)	(4.9)	(5.3)	(8.5)	(.19)	(.029)	(.44)	(5.5)
4	July 1	.27	2.45	11.7	.83	.054	6.1	6.5	11.0	.38	.098	.70	6.9
		(.18)	(1.91)	(7.0)	(.50)	(.041)	(4.9)	(5.1)	(8.1)	(.17)	(.066)	(.44)	(5.5)
7	Monthly	.21	2.19	9.0	.67	.045	4.8	4.8	7.1	.27	.041	.49	5.1
	April 15-June 15	(—)	(1.65)	(—)	(—)	(.032)	(3.7)	(3.5)	(—)	(—)	(—)	(—)	(3.7)
6	Bi-weekly	.17	1.98	8.0	.58	.038	4.0	4.0	6.2	.21	.024	.40	4.3
	April 15-June 15	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)
5	Weekly	.14	1.58	7.0	.51	.031	3.3	2.7	5.3	.14	.019	.26	3.5
	April 15-June 15	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)
42	Bi-weekly	.29	2.86	12.4	1.05	.067	6.7	7.7	13.4	.67	.194	.98	7.6
	June 1-June 15	(.19)	(2.30)	(7.7)	(.72)	(.053)	(5.5)	(6.3)	(10.4)	(.45)	(.162)	(.71)	(6.2)
36	Bi-weekly	.25	2.53	10.6	.84	.054	6.1	6.3	10.6	.46	.103	.75	6.3
	May 15-June 15	(.16)	(1.98)	(6.0)	(.51)	(.041)	(4.9)	(5.0)	(7.7)	(.25)	(.071)	(.48)	(4.9)
31	Bi-weekly	.21	2.07	7.9	.61	.042	4.5	4.3	6.0	.24	.038	.42	4.5
	May 1-June 15	(—)	(1.54)	(—)	(—)	(—)	(3.4)	(3.0)	(—)	(—)	(—)	(—)	(—)
24	Bi-weekly	.20	1.91	7.9	.62	.040	4.2	4.2	7.1	.26	.026	.38	4.6
	May 15-July 1	(—)	(—)	(—)	(—)	(—)	(—)	(2.9)	(—)	(—)	(—)	(—)	(—)
10	Bi-weekly	.12	1.88	8.4	.63	.038	3.9	3.8	5.6	.19	.020	.38	4.4
	April 15-June 1	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)
21	Bi-weekly	.16	1.49	5.9	.43	.029	3.2	2.9	4.8	.11	.018	.25	3.3
	May 1-	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)	(—)
Unwatered	1 inch height	.28	2.50	12.1	.86	.051	5.5	5.6	9.4	.44	.102	.66	6.2
	3 inch height	.27	2.88	15.6	1.11	.064	6.5	6.5	11.6	.52	.134	.94	7.3
Average		.28	2.69	13.8	.98	.058	6.0	6.0	10.5	.48	.118	.80	6.8
Watered	1 inch height	.28	2.50	10.8	.87	.057	5.6	6.0	10.5	.50	.096	.77	6.4
	3 inch height	.29	2.54	11.5	.90	.062	6.1	6.9	11.6	.59	.138	.89	6.9
Average		.28	2.52	11.2	.88	.060	5.8	6.4	11.0	.54	.117	.83	6.6
Average	1 inch height	.28	2.50	11.4	.86	.054	5.6	5.8	10.0	.47	.099	.71	6.3
	3 inch height	.28	2.71	13.6	1.01	.063	6.3	6.7	11.6	.55	.136	.92	7.1
Average	0-6″ depth	0.78	7.20	34.35	2.47	0.16	16.20	16.58	29.32	1.31	0.30	2.09	18.12
	6-12″ depth	0.03	0.41	1.93	0.16	0.01	1.01	1.37	1.82	0.12	0.03	0.19	1.19
	12-18″ depth	0.02	0.21	1.26	0.18	0.01	0.58	0.86	1.17	0.11	0.03	0.16	0.74

*Treatment averages shown in this table are averages for the three soil depths, 0-6, 6-12, and 12-18 inches. Total production may be calculated by multiplying each treatment average and its lower significant limit by three. Likewise the mean squares in table 23 must be multiplied by nine to secure comparable figures for analysis of variance for treatments.

†All plants were clipped on October 1 in addition to dates shown.

‡Figures in parentheses represent lower significant limits (L.S.L.) which serves as a test of significance among means. Any treatment mean of a lower value than the L.S.L. of a higher treatment mean, is significantly lower from that mean at the 5% level (Duncan 1955).

because of continued respiratory losses without compensation through photosynthesis.

EFFECT OF CLIPPING HEIGHT

Forage removal influences chemical content of the roots largely as a result of increased demands for tissue replacement.

Percent protein was significantly higher in roots from plants clipped at 1 in. compared to roots from plants clipped at 3 in. However, present ash and sucrose was significantly higher in roots from plants clipped at 3 in.

Plants clipped at 1 in. had about the same percent cellulose in their roots on both watered and unwatered plots. However, roots from plants clipped at 3 in. had materially higher percent on watered plots (Table 21). Percent cellulose was lower in roots of plants clipped at 1 in. than at 3 in. at both 0 to 6 and 6 to 12 in. depths. At 12 to 18 in. depth, plants clipped at 1 in. had the higher percent.

Both fructosan and reducing sugar were higher in roots from plants clipped at 3 in. than from plants clipped at 1 in. at depths of 0 to 6 in. and 12 to 18 in. but, at 6 to 12 in., roots from plants clipped at 1 in. had a higher percent.

The significant influence of height of clipping upon weight of the various constituents in the roots was largely a result of differences in root yield (Tables 22, 23).

TABLE 23. Analysis of variance for weight of chemical constituents in crested wheatgrass roots from a block of soil 1 ft by 1 ft at 3 depths for various clipping treatments on watered and unwatered plots for data presented in table 22.

Source	Degrees of freedom	Ether extract	Protein	Ash	Calcium	Phosphorus	Lignin	Cellulose	Other carbohydrates	Reducing sugar	Sucrose	Fructusan	Hemicellulose
Water (H_2O)	1	.005	1.38	341.63†	.53*	.0001	.67	6.97	12.33	.20	.0001	.05	.44
Treatment (tr.)	15	.173†	9.86†	465.84†	2.47†	.0078†	56.91†	85.24	399.90†	1.98†	2.0255†	3.73†	93.45†
Height (ht.)	1	.002	2.13*	216.22†	.96†	.0036†	24.79†	38.14†	126.72†	.34	.0668†	2.01†	30.00†
Tr. x ht.	15	.018	.90*	44.47*	.17*	.0006*	2.51	2.04	10.48	.12	.0110†	.08	3.11
Tr. x H_2O	15	.009	.36	33.29*	.17*	.0002	2 03	2.84	10.09	.08	.0016	.10	2.66
Ht. x H_2O	1	.006	1.45	102.01*	.59*	.0010*	2.56	.02	15.89	.01	.0010	.29	5.25
Ht. x tr. x H_2O (a)	15	.013	.33	13.77	.07	.0002	1.53	2.30	11.95	.11	.0007	.15	2.30
Depth	2	12.304†	1,013.83†	22,902.94*	113.00†	.4980†	5,069.31†	5,103.00†	16,521.97†	30.49†	1.6075†	77.67†	6,283.86†
Depth x H_2O (b)	2	.007	.80	283.16†	.42*	.0002	.30	8.17*	15.61	.21*	.0003	.11	.25
Depth x tr.	30	.137*	6.99†	332.19†	1.38†	.0053†	39.24†	53.72†	230.41†	.87†	.1225†	1.54†	61.15†
Depth x ht.	2	.002	1.68*	173.58†	.54*	.0032†	18.06†	29.12†	102.26†	.21*	.0506†	1.57†	22.82†
Depth x Tr. x ht.	30	.020*	.86†	42.31*	.14	.0006†	2.41	1.90	10.65	.09*	.0091†	.07	3.09
Error (c)	62	.010	.34	24.08	.12	.0002	1.53	2.09	9.44	.05	.0011	.08	2.20

*Denotes significance at the 5% level. †Denotes significance at the 1% level.

EFFECT OF FREQUENCY AND DATE OF CLIPPING

Date and frequency of clipping had a significant effect upon chemical content of roots for all constituents except ash, phosphorus, and hemicellulose (Table 21).

Generally, treatments that caused a decrease in total root yield also caused a decrease in weight yield of the various constituents in the roots. However, these treatments that caused a decrease in total root yield, caused an increase in percent of ether extract, protein, lignin, and cellulose (Fig. 11). Plants clipped frequently or late in the growing season contained a higher percent of each of these constituents in their roots than those clipped less frequently or earlier. These findings agree with those of Arny (1932) and Weinmann (1948b).

Numerous investigators have found that soluble carbohydrates in roots are materially decreased with frequent or intense clipping (Aldous 1930b, McCarty & Price 1942, Pierre & Bertram 1929, Weinmann 1943, 1952). Also, harvesting late in the growing season has been found to decrease carbohydrate reserves (McCarty & Price 1942, Sturkie 1930, McCarty 1935).

In the present study, date and frequency of clipping did not significantly affect percent of the other carbohydrate fraction in roots. This might be expected since hemicellulose makes up from 50 to 75% of the other carbohydrate fraction and it was not influenced by treatment. Reducing sugar, sucrose, and fructosan were all significantly affected by both date and frequency of clipping (Table 21). When comparing treatments 19, 18, 15, 12, 8, and 4, clipped only once April 15, May 1, May 15, June 1, June 15, and July 1, respectively, it was found that percentages of reducing sugar, sucrose, and fructosan all showed a general decrease as clipping season was delayed, with the exception of the July 1 clipping. Plants on this date were in early dough stage and may have started to replenish their carbohydrate reserve.

Date of clipping seemed to have less influence upon carbohydrate reserves when the plants were harvested more than once. For example, there were no significant differences in percent content or quantity of reducing sugars, sucrose, or fructosan among plants clipped biweekly from April 15 to June 1,

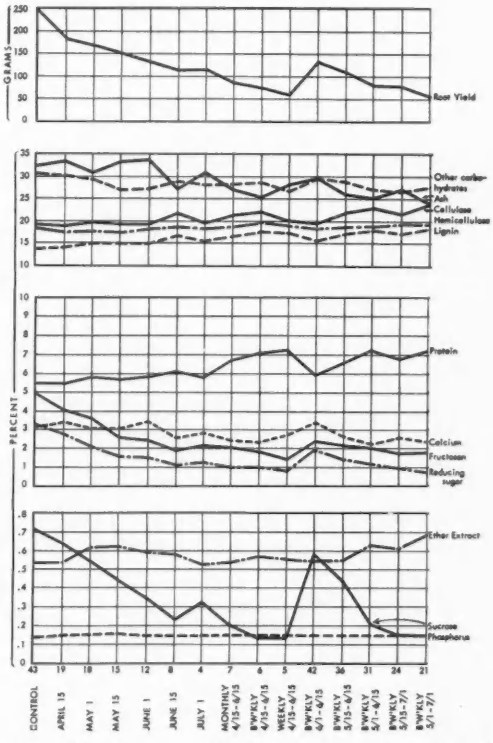

FIG. 11. Average root yield from a column of soil 1 ft square and 18 in. deep and chemical content of roots after a 5-yr clipping period for 15 selected treatments. The chemical content data are unweighted averages of the percentages found at depths of 0-6, 6-12, and 12-18 in.

May 1 to July 1, or May 15 to July 1 (treatments 10, 21, 24) except percent reducing sugar was significantly lower in treatment 24 than in treatment 21.

Increased frequency of clipping or decreased period of time between clippings produced decreased percentages of reducing sugars, sucrose, and fructosan in the roots. For example, in treatments 5, 6, and 7, clipped from April 15 to June 15 at weekly, biweekly, and monthly intervals, roots contained .78, .94, and 1.07% reducing sugar and 1.4, 1.8, and 2.0% fructosan.

Roots from treatment 42 clipped on June 1 and again on June 15 had a higher percentage of sucrose and reducing sugar than roots from treatment 12 clipped only on June 1 or treatment 8, clipped only on June 15. The differences were most pronounced on watered plots and on plants clipped only at 3 in.

Both weight of roots and percentage of reducing sugars, sucrose, and fructosan decreased under frequent and close clipping. Total yield of sugars therefore was reduced even more markedly.

EFFECT OF DEPTH OF ROOT

The percent of ether extract, protein, calcium, phosphorus, cellulose, sucrose, fructosan, and hemicellulose was significantly different in the root samples from different depths (Tables 20, 21). Average percent ether extract, protein, ash, and phosphorus tended to be highest in the roots found in the surface soil and to decrease in samples from deeper depths. Calcium, cellulose, reducing sugars, sucrose, fructosan, and hemicellulose were progressively higher as depth of sample increased.

Because of much greater root weight in the surface soil, all chemical constituents occurred in greater amounts in the surface 6 in. (Table 22).

Percent ash decreased with increase in root depth whereas percent sugar increased. This suggests that increased absorption of minerals is associated with energy of respiration; thus, with greater respiration occurring in the shallower roots, the content of sugar and fructosan would be lowered, whereas the ash content would be raised. This agrees with the findings of Hoagland & Broyer (1936), Broyer (1950), and Hoagland (1937).

Although percent ash in the roots generally was lower at shallower depths, percent calcium was higher. This perhaps resulted because of increased calcium available in the soil at lower depths.

On unwatered plots, percent of other carbohydrates increased from 26.7 at 0 to 6 in. to 27.0 at 6 to 12 in. and 28.4 at 12 to 18 in. On watered plots, these percentages were 29.6, 27.5, and 29.1, respectively. These higher percentages on watered plots were perhaps a result of increased photosynthetic activity under more favorable conditions. Significant interactions between depth and water, in most cases, have no obvious interpretation.

The actul weight of each constituent was closely associated with total root yield at each depth (Table 22).

CONCLUSIONS AND DISCUSSION

Proper grazing is a reflection of both plant and animal responses and, therefore, must be based upon many considerations in addition to percentage of herbage removed. Such factors as herbage yield, seed production, root production, general vigor, and chemical composition are measures of plant responses. Since the latter determines nutrient content, it also indirectly determines animal response. Each of the above plant responses will be determined by the environment under which the plant grows. No one set of conditions could be expected to result in most favorable results for all responses. Climate, soil, and herbage removal have variable and interacting influences upon these responses. The season, frequency, and intensity of grazing not only interact among themselves, but their separate or combined influences upon the plant will depend upon climate and soil. It is impossible to draw a conclusion dealing with the specific effect of any single influence upon plant responses without at the same time interpreting the effects of other interdependent factors.

HERBAGE YIELD

Maximum yield of herbage was obtained from plants clipped only in the fall and minimum yield from plants clipped frequently in the spring. Clipping only once or as many as three times late in the growing season gave the greatest yield excepting the control. But, increasing yield by late season harvesting can only be at the expense of nutritiousness and palatability. Further, late season harvesting tended to cause more rapid decrease in herbage yield from year to year than early season harvesting.

The application of water had little effect upon yield of plants clipped only early in the growing season, but plants clipped later were materially benefited. Growth was increased more by additional water as intensity and frequency of harvesting increased.

Additional water had about the same effect on plants clipped at 1-in. and 3-in. stubble height, except for plants clipped late in the growing season. In this case, plants clipped at 3 in. responded better than plants harvested more closely.

In general, plants clipped at 1-in. yielded less herbage than plants less intensively clipped. However, the control plants and those clipped only once, June 1 or later, produced more when harvested at 1 in.

Frequency of clipping had a profound effect upon production of herbage. Plants clipped weekly from May 1 to July 1 produced an average of 73.1 gm per plant during 5 yrs of treatment, compared to 97.5 and 130.2 gm for plants clipped biweekly and monthly.

Yield also decreased with increased number of clippings. Treatments clipped at weekly intervals beginning April 15 for a total of 9 times, produced an average of 65.1 gm per plant annually over a

5-yr. period, whereas plants clipped weekly from April 15 for a total of only 7 times produced 89.6 gm.

Clipping every week early in the growing season decreased the yield less from year to year than clipping every week late in the season. However, this was not true when plants were clipped at 2 or 3-week intervals.

When plants were clipped only once during the growing season, late season (June 15 & July 1) or early season clipping (April 15 & May 1) produced more dry weight than mid-season clipping (May 15 or June 1).

Even though early-harvested plants produced a lower total yield for 5 yrs. than late-harvested plants, the plants clipped early were producing more herbage at the end of the experiment than plants clipped late. Plants harvested during mid-season were producing the least forage at the end of five years and, likewise, produced the least total forage during the five years. Mid-season harvesting, like late-season harvesting, results in regrowth from latent tiller buds; consequently growth is delayed. As a result, plants harvested in mid-season are deprived of the growth period late in the growing season before summer dormancy, whereas, plants harvested before or after this period are allowed continued growth until summer dormancy approaches.

Growth Rate

Rate of growth following clipping is largely a result of root reserves. Reduced photosynthetic tissue because of close or frequent clipping reduced carbohydrate reserves in the roots and retarded regrowth.

Growth subsequent to harvesting was substantially more rapid on watered plots than on unwatered plots if plants were clipped more than once during the growing season. Regrowth of plants receiving additional moisture was taller and more vigorous. The influence of additional water on regrowth was more pronounced on plants clipped late in the growing season. Likewise, rate of growth was increased more by water as intensity and frequency of clipping increased.

Date and frequency of clipping had significant effects upon both height and vigor of regrowth. Increase in frequency of clipping and delay in date of clipping markedly decreased both height of seed culms and vigor of the plants over a 5-yr period.

Seed Production and Germination

Most treatments producing high forage yields likewise produced high seed yields and high germination. However, this was not true in every case. Plants clipped late in the growing season produced relatively high forage yields but low seed yields.

Plants receiving additional water produced more spikes per plant, but approximately the same number of viable seeds per spike as unwatered plants.

Plants clipped at 3 in. produced slightly more spikes per plant and a slightly greater number of viable seeds per spike than plants clipped at 1 in.

As would be expected, delay in date of clipping decreased the number of spikes and the number of viable seeds per spike. Likewise, increased clipping frequency decreased both the number of spikes and the number of caryopses per spike.

Germination was not significantly different among any of the treatments. Apparently, if vigor of the plant is sufficient for seed production at all, the seed produced is likely to be viable. However, it was noted that seeds from plants lacking vigor were not as large as seed from plants in comparatively high vigor. Therefore, it would appear that vitality of the seedlings would be reduced because of lower food reserve in the seeds.

Forage Value

The nutrient content of herbage is important if the nutritional requirements of grazing animals are to be met. Plants allowed to mature without grazing become less desirable as animal feed. Plants grazed frequently so that growth is renewed periodically will remain comparatively high in nutrients. This high quality, however, may be obtained only at the expense of herbage weight and seed production. For this reason, a fundamental knowledge of the factors affecting nutrient content and forage yield is important in range management.

Plants clipped from April 15 to June 15 yielded the most desirable forage in digestible protein, digestible organic matter, and total digestible nutrients. Forage from plants harvested weekly was somewhat better than from plants harvested biweekly or monthly. However, plants harvested monthly gave highest herbage yields and displayed highest vigor at the end of 5 yrs. Likewise plants clipped biweekly produced more herbage and displayed higher vigor than plants clipped weekly.

In general, herbage from watered plots had higher percentages of ash, calcium, phosphorus, and cellulose. The effect of water on other chemical constituents was dependent on clipping treatments. Herbage harvested either late in the growing season or at frequent intervals was higher in protein, digestible organic matter, and total digestible nutrients on unwatered plots.

Closer clipping during the growing season produced a higher percentage of leafy material; therefore, herbage harvested at 3 in., in most cases, contained higher percentages of cellulose and lignin and lower percentages of protein and ash than herbage harvested at 1 in.

The percentage of the various nutrients in the herbage showed no trend from year to year for any of the treatments. However, average annual yield of each constituent decreased as herbage yield decreased.

The less frequently plants were clipped, the lower the percentages of protein, digestible organic matter, total digestible nutrients, calcium, and phosphorus, and the higher the percentages of lignin, cellulose, and other carbohydrates in the harvested herbage. This, again, was the result of higher percentage of leafy material caused by more frequent clipping.

Frequently-clipped plants maintained a high percentage of protein and total digestible nutrients, but yield or dry matter and, consequently, total yield of protein and digestible nutrients decreased each year. However, since palatability decreases with maturity, a high percentage of a given nutrient might be more important than total production of that nutrient.

As date of initial clipping was delayed, percent of protein, phosphorus, digestible organic matter, and total digestible nutrients decreased, whereas lignin, cellulose, and other carbohydrates increased.

Numerous interactions between height, frequency, and season of clipping emphasize the interdependence of these factors in determining yield of nutrients.

In general, any combination of early and close clipping on unwatered plots resulted in high quality herbage, but quantity declined rapidly each year the plants were harvested. The decline in production from year to year was not as pronounced on watered plots.

Stem-leaf Ratio and Nutrient Content in Fall Growth

Frequently, ranges grazed during the spring are again grazed during the fall. For this reason, the character of the growth available in the fall is important. Forage remaining for fall grazing varies materially in stem-leaf ratio and nutrient content, depending upon the grazing use the previous spring and general growing conditions subsequent to grazing.

Generally, plants clipped late in the growing season or frequently had a higher stem-leaf ratio in the fall on unwatered plots, whereas plants clipped early in the growing season or less frequently had a higher stem-leaf ratio on watered plots.

Differences in chemistry of the herbage remaining in the fall were largely a result of stem-leaf ratio. Leaves were higher in percent protein, ether extract, ash, calcium, and phosphorus, whereas stems were higher in lignin, cellulose, and other carbohydrates.

In general, fall herbage from watered plots was higher in percent protein, cellulose, ash, calcium, and phosphorus in both leaves and stems. Herbage from unwatered plots was higher only in ether extract and lignin. In most cases, both stems and leaves of plants previously clipped at 1 in. were higher in percent protein and phosphorus, whereas those from plants clipped at 3 in. were higher in ether extract and lignin.

When plants were harvested only once during the growing season, delay in clipping resulted in higher percentages of protein, ether extract, ash, calcium, and phosphorus in both stems and leaves of autumn herbage. Percentages of cellulose and lignin were decreased by delayed clipping.

Root Growth

Knowledge of the root system aids materially in explaining resistance of plants to grazing and drought. Obviously, an extensive root system is conducive to plant survival during drought. In regions of dry summers, the soil dries out from the surface downward as the summer progresses and, therefore, a shallow root system with fewer roots would have considerably less moisture available than a deep root system composed of many roots.

In general, treatments that produced the greatest herbage yield likewise produced the greatest root yield. Plants in high vigor displayed a well-developed root system. It appears that any herbage removal reduces total root production. However, certain harvesting treatments minimized this reduction. The effect of forage removal was dependent to a large extent on soil moisture and general growing conditions.

Plants clipped at 1 in. had a slightly greater average weight of roots when watered, whereas plants clipped at 3 in. produced a greater weight of roots when unwatered. In general, plants clipped at 3-in. height produced a greater weight of roots than plants clipped at 1-in. height. Reductions in weight of roots because of closer clipping occurred in all three soil depths, 0 to 6, 6 to 12, and 12 to 18 in. but were more pronounced in the 0 to 6 in. depth.

When plants were clipped only once during the growing season, the root weight was reduced as the date of clipping was delayed until late-season June 15. Thereafter, there was little change in root yield as the date was delayed. Mid- and late-season harvesting apparently leave little time for herbage replacement before summer dormancy; hence food manufacture is limited and root growth retarded.

Both frequent clipping and late-season clipping caused a significant decrease in weight of roots.

Unwatered plants had fewer roots and a more shallow concentration of roots than plants receiving water.

There was little difference in the depth of root concentration for plants clipped at different heights on watered plots, but on unwatered plots, the plants clipped at 3 in. concentrated their roots at a much greater depth.

When plants were clipped only once during the growing season, later clipping materially reduced both the number and depth of roots. These reductions were greater for plants harvested at 1 in. than for those harvested at 3 in. Plants clipped many times at weekly intervals had fewer roots and shallower root penetration than plants clipped fewer times at monthly intervals. These differences were greatest for unwatered plants and for plants clipped at 1 in.

An important fact evident from these studies is that the volume of soil from which moisture and nutrients can be absorbed is determined by forage utilization.

Root Reserves

Little is actually known about food storage in roots. It is not clearly understood which organic materials constitute food reserves. It is, however, agreed that the more soluble forms of carbohydrates are most important. Primary uses of reserves are for meeting the general physiological needs of the plant

during periods of stress, for regrowth following herbage removal, and for the production of initial growth in the spring. Root reserves are associated with rate of herbage growth and general vigor of the plant. Plants in high vigor would be expected to have a comparatively high carbohydrate reserve and during favorable conditions to grow at a much faster rate.

In this study, roots from watered plants had higher percentages of phosphorus, cellulose, sucrose, reducing sugars, and fructosan, whereas roots from unwatered plants were higher in protein and ash. Greater photosynthetic activity in watered plants may account for the higher sugar content in the roots. There was little difference in percent of cellulose or sucrose between roots from watered and unwatered plants when clipped at 1 in., but when clipped at 3 in., both were higher in roots from watered plants.

Both water and height of clipping had an effect upon percent of reducing sugars in the roots at different depths. On unwatered plots the roots contained about the same percent at all depths, but on watered plots the percent increased with increased depth. Roots from plants clipped at 1 in. were lower in percent of reducing sugars than roots from plants clipped at 3 in., except at the 6-12 in. depth.

Generally, treatments such as frequent and late clipping that caused a decrease in root yield caused an increase in percent ether extract, protein, lignin, and cellulose in the roots.

Increased frequency of clipping or decreased period of time between clippings produced decreased percentages of reducing sugars, sucrose, and fructosan in the roots.

Percent ether extract, protein, ash, and phosphorus tended to be highest in the roots near the soil surface. Calcium, cellulose, reducing sugars, sucrose, fructosan, and hemicellulose were progressively higher as depth of sample increased.

SUMMARY

During the years 1948 to 1953 a study was conducted near Logan in northern Utah to determine the effects of season, intensity, and frequency of herbage removal upon crested wheatgrass under watered and unwatered conditions.

Data were collected on herbage yield, rate of growth, vigor, seed production, chemical content of herbage, root yield, and chemical content of roots.

It is difficult to draw conclusions about the specific influence of any one of the main effects studied. Response to any one factor must be interpreted in light of the combined effect of all factors.

Herbage and seed yield. In most cases, plants receiving additional water produced more herbage than unwatered plants.

Generally, yield from plants clipped at 3 in. was greater than from plants clipped at 1 in. However, plants clipped late in the growing season tended to produce more when harvested at 1 in.

In all cases, increased frequency of clipping decreased yield of herbage, but the extent was dependent upon date and number of clippings, and the application of water.

Regrowth of herbage after clipping was more rapid on watered plots than on unwatered plots. Increased frequency and increased intensity of clipping reduced plant vigor and rate of growth. These were more pronounced on unwatered plots than on watered plots.

The number of filled caryopses per spike and spikes per plant were increased by additional water and by decreased frequency or decreased intensity of clipping. Delay in date of clipping greatly decreased the number of filled caryopses per spike and the number of spikes per plant.

Germination of seeds was not significantly affected by clipping treatments.

Chemical content of herbage. The percentage of the various nutrients in the herbage of a given treatment showed no significant trend from year to year.

Additional water increased the percentages of ash, calcium, phosphorus, and cellulose in most treatments and, in general, forage harvested at 3 in. contained a higher percentage of cellulose and lignin, and a lower percentage of protein than forage harvested at 1 in.

Plants clipped less frequently had lower percentages of protein, digestible organic matter, total digestible nutrients, calcium, and phosphorus, and higher percentages of lignin and other carbohydrates.

As the season advanced, herbage increased in percent of ether extract, lignin, cellulose, and calcium, but decreased in percent protein, phosphorus, digestible organic matter, and total digestible nutrients.

In most cases, any combination of early and close clipping resulted in high quality herbage, but quantity declined rapidly each year the plants were harvested.

Character of fall herbage. Difference in chemical content of the herbage remaining in the fall, following spring clipping, were largely a result of stem-leaf ratio. Leaves contained more protein, ether extract, ash, calcium, and phosphorus, whereas stems contained more lignin, cellulose, and other carbohydrates.

In general, both stems and leaves from the fall herbage were higher in percent protein, cellulose, ash, calcium, and phosphorus on watered plots, whereas herbage from unwatered plots was higher in ether extract and lignin. Both stems and leaves were higher in percent protein and phosphorus from plants clipped at 1 in., whereas plants clipped at 3 in. were higher in ether extract, lignin, and calcium.

Plants harvested most frequently during the growing season produced herbage in the fall that was more leafy and, consequently, higher in percent protein, ether extract, ash, calcium, and phosphorus and lower in lignin, cellulose, and other carbohydrates than herbage less frequently harvested.

Root yield. Plants clipped at one inch produced greater quantities of roots when watered, whereas

plants clipped at three inches produced greater quantities when unwatered. However, root yield from plants clipped frequently until late in the growing season was not affected by either height of clipping or additional water.

Root yield was reduced as date of harvesting was delayed and as frequency of clipping was increased. Frequency, intensity, and date of clipping all had greatest effect upon root yield in the surface 6 in. of soil, compared to deeper depths.

Increased frequency of clipping and delayed date of clipping reduced both the number of roots and depth of root penetration. These reductions were more pronounced on unwatered plots, compared to watered plots.

Chemical content of roots. Roots from plants receiving additional water had significantly higher percentages of phosphorus, sucrose, cellulose, and other carbohydrates, whereas roots from unwatered plants had significantly higher percentage of protein and ash.

Percentages of cellulose, fructosan, and reducing sugar were higher in roots from plants clipped at 3 in. at 0 to 6 in. depth, but at deeper depths plants clipped at 1 in. had higher percentages.

In general, treatments that caused decreases in root yield caused increases in percent ether extract, protein, phosphorus, lignin, cellulose, and calcium, and decreases in percent reducing sugar, sucrose, and fructosan in the roots. Roots from plants clipped frequently or late in the growing season were low in reducing sugar, sucrose, and fructosan.

Percentages of ether extract, protein, ash, and phosphorus were highest in roots from the surface 6 in. of soil and lowest in deeper layers. Percentages of calcium, cellulose, reducing sugars, sucrose, fructosan, and hemicellulose were higher in deeper root samples and lower in shallower root samples.

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THE TRANSFORMATION OF ENERGY BY *DAPHNIA PULEX*

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INTRODUCTION

Since Lindeman (1942) developed his classic concept of community dynamics, there has been considerable interest in measuring the rate of energy transfer in aquatic systems. This work, however, has been greatly hindered by the lack of quantitative data concerning energy relationships of the trophic levels. In particular, little information has been obtained concerning the primary consumer level. Therefore, a laboratory study of energy transformation by a primary consumer was undertaken.

Daphnia pulex var. *pulicaria* Forbes was used as the primary consumer. This animal was readily available in a laboratory culture. The ease in culturing, its short life cycle, lack of free egg or larval stages, genetic homogeneity through parthenogenetic reproduction, and absence of social complexity make *Daphnia* particularly suited to laboratory studies (Slobodkin 1954). The organism fed to *Daphnia* was *Chlamydomonas reinhardi* Dangeard. This green alga is easily grown in pure palmella cultures on nutrient agar.

It has been well established that in any biologically closed system the total energy input is equal to the total energy output. In this study the problem was to measure the amount of energy consumed by the *Daphnia* and to determine how much of this energy went into growth and production of young, and how much was lost as heat during the animal's daily activities. The amount assimilated could then be determined by the sum of growth and respiration, and the energy lost in egestion, including unassimilated material and metabolic waste products, by the difference between ingestion and assimilation. From these measurements the efficiency of converting consumed energy into new protoplasm (gross efficiency) and assimilated energy into new protoplasm (net efficiency) could be ascertained. To determine the effect of different concentrations of available food on the energy budget, four concentrations of food were employed in the experimental studies, all of which were carried out in the absence of light and at 20°C.

Few studies have been made on the energy relationships in primary consumer organisms. Ivlev (1939a) studied the transformation of energy by *Tubifex tubifex*. Since this organism feeds on detritus, its position as a primary consumer, in the strictest sense, can be questioned. Trama (1957) studied the balance of energy in nymphal forms of *Stenonema pulchellum*. This represents the first study on energetics in an aquatic browsing herbivore. To the writer's knowledge no complete study of energy transformation has been made on a zooplankter. Quantitative studies on natural zooplankton populations have been made by Juday (1940), Pennak (1946), Edmondson (1946), Riley (1947, 1949) and others but these have not dealt directly with the energy dynamics of these populations. Studies on the dynamics of production in aquatic communities have been made by Juday (1940), Lindeman (1941, 1942), Clark (1946), Dineen (1953), Harvey (1950), and

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Odum (1955, 1957). These studies, which certainly have made definite contributions to our understanding of trophic dynamics, demonstrate the need for more precise information on the calorific values of aquatic organisms. Because this information was not available these investigators and others had to convert standing crop data in terms of biomass to energy values by means of approximated calorific constants, or by some other indirect means of computation. MacFadyen (1948) pointed out that due to lack of data we rarely know the calorific values by which to multiply biomass figures, and, in practice, these values are assumed to be constant for a large group of diverse organisms. He further indicated that confusion has resulted from the common practice of implying that energy flow and biomass flow are synonymous. Energy and biomass cycles are fundamentally distinct. Energy passes through an ecosystem and is used only once by an organism whereas matter is either in circulation continuously or in storage (MacFadyen 1948). Because of the lack of data Lindeman (1942) used the respiratory correction of Ivlev (1939a) to correct the herbivore production value for energy lost in respiration. Since then Ricker (1946) and Trama (1957) have indicated that Lindeman's corrections for respiration are probably too low.

There has been considerable confusion in the definition of consumer productivity since Lindeman and Hutchinson (Lindeman 1942) formulated their concept of aquatic production. They, like Clarke (1946, 1954), have schematically designated the fate of the energy which enters the community in the form of solar radiation. These workers defined herbivore production as the rate of energy uptake from the primary producers. H. T. Odum (1956a) pointed out that production in this sense is quite different from the widely accepted idea of production as the rate of synthesis of organic matter and suggested that the latter definition be used rather than the rate of consumption by a particular trophic level. With my experimental design, Odum's definition was more meaningful than Lindeman's and was the one used.

Primary productivity studies, to mention a few, have been made by Edmondson (1955b), Manning and Juday (1941), H. T. Odum (1956b), Penfound (1956), Riley (1938, 1939, 1940, 1941, 1944, 1949), Ryther (1954a), Steeman Nielsen (1951, 1952) and Verduin (1951, 1956a, 1956b). Much of the literature on fish production has been reviewed by Ricker (1946). Gerking (1952, 1954) studied the protein metabolism of sunfishes and bluegills. In many of these studies on fish production the lack of calorific data is evident.

The complex nature of aquatic food webs is discussed by Allee *et al.* (1949), Elton (1951), Welch (1952) and E. P. Odum (1953). The dynamic community concept of Lindeman (1942) and others is admittedly an oversimplification because of this complexity. Lindeman's basic concept, however, is in agreement with thermodynamic principles. The incorporation of the full complexity of community dynamics into Lindeman's scheme is yet to be accomplished.

Dr. D. C. Chandler, University of Michigan, under whose direction this work was carried out, gave much help and encouragement throughout this study. Dr. L. B. Slobodkin gave many stimulating ideas and originally interested me in the general problem. Dr. F. E. Smith was most patient in discussion and gave considerable advice for the evaluation of the results. Drs. J. E. Bardach and A. S. Sussman kindly read the manuscript and made helpful suggestions. Drs. J. M. Allen, E. R. Baylor, W. R. Dawson, G. H. Lauff, and R. E. Townsend were most helpful in working out techniques and in making equipment available. Dr. S. D. Gerking, University of Indiana, aided in the formulation of the bomb calorimeter technique. The *Daphnia* were originally identified by Dr. J. L. Brooks, Yale University, and provided by Dr. Slobodkin for this study. Dr. G. W. Saunders helped with the Russian translations and Mr. R. A. Main kindly constructed the graphs. To these and many others who have not been named, I express my deep gratitude.

METHODS

Energy Input

Calorific value of the algae. The green alga, *Chlamydomonas reinhardi*, was used for feeding *Daphnia pulex* in the experimental work. It was grown on sterile nutrient agar plates consisting of Beyerinck's solution, soil extract, ferric chloride, and agar as described by G. M. Smith (unpublished) and listed by Slobodkin & Richman (1956). The Beyerinck's solution was modified by adding phosphate buffer (6 ml M/15 K_2HPO_4 and 4 ml M/15 KH_2PO_4 per 1000 ml).

After inoculation, the plates were placed under a bank of fluorescent lights with an intensity of 25 foot-candles in a constant temperature room. The temperature of the room was set at 20°C ±1°C. The temperature of the culture under the lights was 24 ±1°C. After 4 days the plates were flooded with sterile water. With this algal suspension new plates were inoculated and the remainder centrifuged for 5 minutes at approximately 3000 rpm. The centrifugate was dried at 60°C for 24 hours and stored in weighing bottles in a desiccator until the calorific analysis was made. Each plate, 6 inches in diameter, gave an algal yield of approximately 10 mg oven dry weight.

The calorific value of the algae was determined with a micro-oxygen bomb calorimeter. The bomb is approximately one-fifth the size of a standard oxygen bomb, having an internal volume of 70 ml. It consists of a thick walled metal vessel lined with platinum and a bomb head of the single valve type. Two electrodes are attached to the under side of the head including a straight electrode and a loop electrode. The straight electrode is hollow and makes connection with the oxygen inlet allowing the oxygen

to enter below the combustion capsule. The loop electrode holds the combustion capsule. Both electrodes make contact with outside terminals and serve as binding posts for the fuse wire which is strung between them and bent down into contact with the sample. A transformer with a secondary electric current of 10 volts at 5 amperes is attached to the outside terminals and provides current for the ignition of the sample.

After placing the sample in the bomb and charging it with oxygen, it is placed in the water bucket and put into the calorimeter jacket (Parr Manual No. 120, 1948). Water circulation around the bomb is provided by a stirrer which is attached to an upright on the jacket and is moved vertically at a constant rate by a motor geared down to 80 rpm. The thermometer, immersed in front of the bomb in the water bucket, was a Beckmann differential type graduated to 0.01°C and by means of a reading lens permitted the estimation of thousandths of a degree (Uber 1950).

The water equivalent of the bomb and the calorific value of the algae were determined by a modification of the method described by the Parr Instrument Co. (Parr Manual No. 120, 1948). For the water equivalent, approximately 300 mg samples of standard benzoic acid with a heat of combustion of 6318 cal/gm, were used. All samples of benzoic acid and algae were weighed on an Ainsworth semi-micro keyboard balance accurate to 10 micrograms.

With the bomb calorimeter used, approximately 300 mg of material was needed to obtain a sufficient temperature rise. Since a limited amount of algae was being produced, it was impractical to use this much material for each analysis. On a suggestion from Dr. Gerking. Indiana University (personal communication), about 50 mg of algae were used per run combined with 250 mg of benzoic acid. In this way algae were being conserved and the total sample was sufficient to obtain a large enough temperature rise.

The benzoic acid was added first to the combustion capsule. After partially fusing it on an electric hot plate it was cooled and weighed. To this the dried algal sample was added from a tared weighing bottle. This bottle was then reweighed to determine the weight of the sample. After placing 0.25 ml of distilled water in the bomb and attaching 7 cm of Parr fuse wire to the electrodes, the combustion capsule was placed in the loop electrode and the wire was arranged so that it just touched the algae. The bomb was closed tight with a special wrench and vise and charged with oxygen at twenty atmospheres. After connecting the transformer wires the bomb was placed in the water bucket containing 1000 ml of distilled water. The combustion procedure is given in the Parr Manual (1948).

Since the calorimeter was not adiabatic, corrections had to be made for radiation gain and loss. These corrections and those due to the burning of the wire and the formation of nitric acid are given in the Parr Manual. The temperature rise, corrected for radiation gain and loss, multiplied by the water equivalent gave the total calories produced in the combustion. From this were subtracted the calories produced due to benzoic acid, burning of the wire, and formation of nitric acid to give the net heat liberated in the combustion.

Because only one-sixth of the total sample was *Chlamydomonas* and the other five-sixths benzoic acid, it was decided to make some analyses with *Chlamydomonas* alone. For these determinations the sample size per analysis was approximately 230 mg of algae. The procedure was the same as described above except the benzoic acid was omitted.

Nitrogen and ash content of the algae. Determinations of nitrogen were made according to the micro-Kjeldahl procedure of Niederl & Niederl (1942). A Pregl-Parnas-Wagner steam-distillation apparatus was used. Digestions were performed on a micro-Kjeldahl digestion shelf. Six determinations were made with sample sizes ranging from 12 to 35 mg of algae dry weight.

The percentage of ash in the algae was obtained by weight loss on ignition. Samples of approximately 25 mg of dried algae were weighed in crucibles and put in an electric furnace at 600°C for 30 minutes. After cooling, the samples were reweighed and the percentage of ash calculated (Welch 1948).

Weight of the algae. The weight per algal cell was determined by drying and weighing a known volume of an algal suspension of known cell concentration. The cells of the algal suspension were killed by placing them in hot water. Cell concentration was then determined by means of a Spencer bright-line haemacytometer. Twenty cell counts of 0.04 mm^3 haemacytometer fields per sample were made. Five ml of the suspension were placed in a crucible, dried at 60°C for 24 hours, weighed, and the weight per algal cell calculated.

Filtering rate. The filtering rates of 0.7, 1.3, and 1.8 mm female *Daphnia* at food concentrations of 25, 50, 75, and 100 thousand *Chlamydomonas* cells per ml were determined according to the method described by Gauld (1951) and later used by Ryther (1954b) and Conover (1956). The feeding experiments were conducted in the dark in a constant temperature room set at 20° ±1°C. Sterile *Chlamydomonas* cells grown on agar plates were suspended in aerated water left standing in a concrete tank for several months. The cell concentration was determined by taking the mean of a series of haemacytometer counts. The suspension was then diluted to produce the desired concentration. Fifty ml of the food were placed in each of six 100 ml wide-mouth jars. Then *Daphnia* having an average length of 1.8 or 1.3 mm were placed in 5 of these after they were adapted to the experimental conditions for 24 hours. The sixth jar served as a control. For the 0.7 mm *Daphnia* 25 were used instead of 10. The same procedure was followed for each of the 4 food levels, giving a total of 60 experimental jars, 15 at each food level. The experimental and control jars were wrapped in aluminum foil and

placed in the constant temperature room for 24 hours. After this time sub-samples were removed and placed in hot water to kill the cells. The amount of water filtered per day by the *Daphnia* was determined from the difference in haemacytometer cell counts between experimental and control jars using the equation:

$$F = v\ (\ln C_o = \ln C_t)$$

after Conover (1956), where F is the amount of water swept free of food in 24 hours, v the volume of water per animal in the experimental jar, C_t the experimental cell concentration after 24 hours, and C_o the control cell concentration.

Energy Output

Oxygen consumption. Two methods of measuring oxygen consumption were used. The Warburg constant volume type respirometer as described by Umbreit *et al.* (1949) was used in some measurements. Fifty *Daphnia* were placed in 15 ml Warburg respiratory flasks in 5 ml of water with KOH in the center well and oxygen consumption measured for one hour at 20°C. Even though the flasks were shaken the daphnids were almost always caught in the surfare film. Because of this and the small volume of water per animal, it was felt that oxygen uptake was being measured under highly abnormal conditions. More extensive measurements were made with the water bottle method described by Marshall *et al.* (1935) and later used by Conover (1956).

Daphnia were grown in a stock aquarium on a mixture of green algae; these were present in excess of the feeding requirements. Twenty-four hours before the experiment, a group of *Daphnia* was selected for uniformity of size and placed in filtered water at 20°C. Depending on size, 50-100 of these were placed in glass stoppered wide-mouth bottles of approximately 135 ml volume filled with conditioned water. A siphon arrangement similar to that described by Marshall (1935) was used to flush the bottles with 300 ml of the conditioned water. With each set of bottles a control was prepared in the same manner except that no animals were added. The bottles were wrapped in aluminum foil and placed in a constant temperature room at 20°C for 24 hours. At the end of each experiment the water in the bottles was siphoned into 70 ml glass-stoppered bottles. Silk bolting cloth at one end of the siphon prevented the escape of animals from the experimental bottles. The oxygen content of the sub-sample bottles was determined by the Winkler method modified for use with the 70 ml volume (American Public Health Association 1955). The difference in oxygen content of the experimental and control bottles was due to oxygen up-take by the *Daphnia*. The Winkler titrations were made with a 10 ml microburette graduated in fiftieths of a ml using 0.01N sodium thiosulfate.

A series of experiments was designed to determine the relation between feeding and oxygen consumption. The method of preparing the animals was similar to that used by Conover (1956). A quantity of adult female *Daphnia* selected for uniform size was placed in two 1000 ml beakers containing conditioned water. The animals in one beaker received an excess of *Chlamydomonas* while those in the other beaker were not fed. Every day for 5 days the respiratory rates of the fed and unfed *Daphnia* were measured in the dark at 20°C.

Length-weight relationship. After the oxygen analysis, the *Daphnia* in the experimental bottles were used to determine a length-weight relationship. The method was that of Edmondson (1955a). The live animals were removed from the experimental bottle, rinsed in distilled water, placed on a slide and measured with an ocular micrometer. They were then placed on a weighed cover slip, dried for 24 hours at 60°C, cooled in a desiccator and weighed immediately.

Carbon dioxide production. Carbon dioxide production was measured according to the method of Verduin (1951) by converting pH changes to changes in carbon dioxide. The same bottles as in the oxygen uptake experiments were used to measure the change in pH due to carbon dioxide production during the 24-hour experimental period. A Beckman Model G pH meter was used with 5-in electrodes. As mentioned in the oxygen consumption section, wide-mouth glass stoppered bottles were used to accommodate these electrodes. At the end of the experimental period, the contents of the bottles were thoroughly mixed by shaking and the pH measured, care being taken to avoid disturbance of the sample and loss of animals while inserting the electrodes.

A titration curve was made by titrating 1 ml aliquots of 0.01N HCl into 500 ml of conditioned water, After each addition, the pH was measured. At regular intervals a new titration curve was made to check the water for changes in buffering capacity. By means of the carbon dioxide-pH relationship the carbon dioxide production of the *Daphnia* was obtained from the difference in pH between the experimental and control bottles.

Energy Utilization for Growth

Calorific value of Daphnia. The *Daphnia* were maintained in a 25 gallon aquarium. Large stocks were produced by heavy feeding of green algae, primarily *Ankistrodesmus*. Before collecting the daphnids for calorific analysis, they were not fed for a period of at least two weeks. This was done to allow the daphnids to consume the excess food, and in most cases the animals' intestines were empty after this time. The contents of the stock tank were siphoned through a No. 0 silk bolting cloth net into a number of smaller aquaria. This separated most of the young animals, 0.6-0.8 mm, from the other size groups. These were then concentrated by means of a Wisconsin plankton net made with No. 25 silk bolting cloth. The two other size groups, 1.2-1.4 mm and 1.7-2.0 mm, were separated by hand picking with an eye dropper. To facilitate this, collections were made when one size group was predominant in the stock tank. Each group was rinsed several times with distilled water and dried at 60°C for 24 hours. They

were stored in weighing bottles in a desiccator until the calorific analysis was made. With each collection, 50 or more *Daphnia* were measured with an ocular micrometer to determine the average size of the group.

The calorific value of the daphnids was determined in the same way as the *Chlamydomonas*. Samples ranging in weight from 10-25 mg were used combined with enough benzoic acid to make a total sample of approximately 300 mg. Six analyses of each size group were made, for a total of 18 determinations.

Growth rate. The growth rate of the daphnids was determined at four different food levels—25, 50, 75, and 100 thousand *Chlamydomonas* cells per ml. A modification of the method of Anderson *et al.* (1937) was used. Individual new born *Daphnia* were isolated no more than 6 hours after being released by the mother and measured with an ocular micrometer. Each individual was placed in a vial containing 10 ml of food adjusted to the desired food concentration and placed in the dark at 20°C. Every day the animals were placed on a depression slide and enough water removed to prevent them from moving. The total length of the daphnids was measured with an ocular micrometer, each division being equal to 0.039 mm. This measurement consisted of the longest dimension of animal from the anterior-most extension of the head to the inflection point of the concavity joining the ventral edge of the valves to the shell spine (Brooks 1953). Before daily measurements were made cast carapaces and the young released were counted. After the measuring was accomplished the individual animal was placed in a new vial of fresh food. Seven animals were studied at each food concentration.

RESULTS

Energy Input

Calorific value of the algae. The calorific values of *Chlamydomonas reinhardi* using benzoic acid in the determinations are given in Table 1. The average of 12 analyses is 5289 cal/gm dry weight with a range of 5173 to 5500 cal/gm, a standard deviation of ±95.6 and a coefficient of variation of 1.8%. On an ash-free dry weight basis the average calorific value is 5506 cal/gm, the ash content of the algae being 3.94%.

Lower calorific values were obtained when benzoic acid was not combined with the sample (Table 2). The average of 5 determinations is 283 cal/gm less than when benzoic acid was used. On examining the combustion capsule after each combustion a carbonaceous deposit was observed. To check for incomplete combustion the capsule was put in an electric furnace at 600°C for 30 minutes after some of the combustions. This showed that 0.44% of the benzoic acid sample, 0.56% of the algae plus benzoic acid sample, and 4.63% of the algal sample were incompletely burned in the bomb calorimeter. After correcting the results of the algal sample for incomplete combustion by 4.63%, the average becomes 5249 cal/gm dry weight, 40 cal/gm less than the average of the benzoic acid plus algal samples. This difference is considerably less than the standard deviation of either group. Thus the benzoic acid was needed not only to obtain a measurable temperature change but also to bring about complete combustion of the algae.

Table 1. Calorific value of *Chlamydomonas reinhardi* using benzoic acid in the combustion.

Analysis No.	Calorific Value	
	Dry weight (cal/gm)	Ash-free dry weight (cal/gm)
1	5500	5724
2	5305	5522
3	5335	5554
4	5363	5583
5	5251	5466
6	5302	5520
7	5230	5444
8	5309	5527
9	5174	5386
10	5173	5385
11	5178	5391
12	5353	5573
Mean	5289	5506
St. dev.	95.6	99.8
Coef. of var.	1.8%	1.8%

Table 2. Calorific value of *Chlamydomonas reinhardi* without benzoic acid in the combustion.

Analysis No.	Calorific Value (cal/gm dry wt)		Calorific Value (cal/gm ash-free dry wt)	
	Uncorrected	Corrected for incomplete combustion (4.63%)	Uncorrected	Corrected for incomplete combustion (4 63%)
1	5042	5287	5249	5503
2	4992	5235	5197	5449
3	5233	5487	5447	5712
4	4973	5214	5177	5428
5	4790	5022	4968	5228
Mean	5006	5249	5208	5464
St. dev.		148.8		154.9
Coef. of var.		2.8%		2.8%

Calorific values of algae determined by bomb calorimetry have not been reported in the literature. Other workers, however, have reported the percentages of carbohydrate, fat and protein of various algae from elementary analysis. A summary of the elementary composition of a number of algal organisms is given by Vinogradov (1953) and Ryther (1956). Spoehr & Milner (1949) described a method for converting the percentages of C, H, O and N to carbohydrate, fat, and protein. From the relative amounts of C, H, and O they calculated the degree of reduction or R value, which was the percentage of the degree of reduction of methane which has an R value of 100. With the R value and the nitrogen content one can calculate the percentage of carbohydrate, fat, and protein. Spoehr & Milner gave an R value for *Chlamydomonas* of 35.27. Using the ash and nitrogen values determined in my study of 3.94%

and 3.95% respectively and the R values of Spoehr & Milner, the relative amounts of carbohydrate, fat, and protein were calculated. When undergoing complete oxidation in the bomb calorimeter carbohydrate, fat, and protein yield an average heat of combustion of 4.10, 9.45 and 5.65 kcal/gm respectively (Hawk, Oser & Summerson 1954; Sherman 1952). Using these values, the carbohydrate, fat, and protein amounted to 5.155 cal/gm dry weight or 5.366 cal/gm ash-free dry weight. These values determined from the percentages of fat, carbohydrate, and protein are very close to the averages in Table 1 and the corrected averages in Table 2 determined by bomb calorimetry.

Ketchum & Redfield (1949) determined the percentages of C, H, O, N by means of elementary analyses for a number of green algae. Using Spoehr & Milner's formula they calculated the percentages of carbohydrate, fat, and protein on an ash-free basis. From these values one can calculate the calorific values of these algae. Table 3 gives a comparison of the combined results of Tables 1 and 2 with the results of Ketchum & Redfield expressed in cal/gm.

TABLE 3. Calorific value of selected Chlorophyceae.

Organism and Reference	No. of Anal.	Calorific Value		% Ash
		Dry wt (cal/gm)	Ash-free dry wt (cal/gm)	
Chlamydomonas reinhardi	17	5269	5485	3.94
St. dev.		116	123	
Coef. of var.		2.2%	2.2%	
Chlorophyceae Ketchum & Redfield (1949)				
Stichococcus bacillaris	6	5236	5859	9.61
Chlorella pyrenoidosa	7	5444	6182	11.93
Chlorella vulgaris	1	5181	5914	12.40
Scenedesmus obliquus (1)	1	5158	6273	17.78
Scenedesmus obiquus (2)	1	5507	6328	12.98
Scenedesmus brasiliensis	1	5453	6366	14.34
Mean Chlorophyceae	17	5340	6154	
St. dev.		150	217	
Coef. of var.		2.8%	3.5%	

The average calorific value of the Chlorophyceae studied by these workers is 669 cal/gm greater than *C. reinhardi* on an ash-free dry weight basis. On a dry weight basis, however, the average value is only 71 cal/gm greater than *C. reinhardi*. Thus the large difference on an ash-free dry weight basis is accountable by the variation in the ash percentage of these organisms. It is also of interest to note that the coefficient of variation for Ketchum & Redfield's work is 2.8% on a dry weight basis whereas it is 3.5% on an ash-free dry weight basis. This indicates less variation on a dry weight basis and suggests this unit is more suitable for comparison of organic composition or total calorific value.

Weight of the algae. The weight of the *Chlamydomonas* was determined on cell concentrations ranging from 7×10^6 to 32×10^6 cells per 5 ml sample. The mean weight was 0.248×10^{-6} mg per *Chlamydomonas* cell ± a standard deviation of 0.017×10^{-6}. The coefficient of variation was 6.8%.

The mean calorific value of one *Chlamydomonas* cell and its standard deviation was calculated by converting biomass to energy using the mean calorific value for the algae of 5269 cal/gm (Table 3). These values were 1.308×10^{-6} cal/cell ± 0.088×10^{-6}.

Filtering rate. The volume of water swept free of cells is independent of the concentration of food for a given size group over the range of food concentrations employed (Table 4). For a four-fold increase in the concentration of *Chlamydomonas* the volume of water filtered was essentially constant.

TABLE 4. Volume of water filtered by *Daphnia* feeding on 4 concentrations of *Chlamydomonas*.

Approximate mean concentration of *Chlamydomonas* (Cells/ml)	Length (mm)	Dry weight (mg)*	Volume filtered (ml/Daphnia/day)	Volume filtered (ml/mg/day)
25,000	0.68	0.003	0 [illegible]	303.33
50,000	0.71	0.003	0.[illegible]7	2[illegible]0.00
75,000	0.72	0.003	0.99	330.00
100,000	0.69	0.003	0.83	276.67
Mean	0.70	0.003	0.90	300.00
25,000	1.31	0.015	4.10	273.33
50,000	1.34	0.016	4.20	262.50
75,000	1.30	0.015	3.99	266.00
100,000	1.26	0.014	3.41	243.57
Mean	1.30	0.015	3.93	262.00
25,000	1.77	0.028	5.15	183.93
50,000	1.86	0.030	5.53	184.33
75,000	1.81	0.029	5.11	176.21
100,000	1.75	0.027	4.81	178.15
Mean	1.80	0.0285	5.15	180.70

*Weights taken from length-weight relationship (Fig. 3).

The independence of filtering rate and food supply is also shown in Fig. 1, where the filtering rates at the 4 food concentrations are plotted against the weight of the *Daphnia*. This figure also shows the relationship between the size of the animals and the filtering rate. As the daphnids increase in size the filtering rate per animal increases in a curvilinear fashion with the rate leveling off as the animal gets larger. On a dry weight basis food consumption is inversely related to the size, the 0.7 mm *Daphnia* filtering an average of 300.0 ml/mg/day, and the 1.3 mm size group 262.0 ml/mg/day, and the 1.8 mm animals 180.7 mil/mg/day. These relationships between filtering rate and size are similar to those of Ryther (1954b) on the filtering rate of *Daphnia magna*.

Few studies have been made on the feeding rate of fresh-water filter-feeding zooplankton. Ryther's study (1954b) represents the only quantitative study of this sort available in the literature. He reports a range of filtering rates from a maximum of 81 ml/animal/day to a value close to zero depending on the concentration and the age of the phytoplankton population used for food and the period of feeding prior to the experiment. In the range of food con-

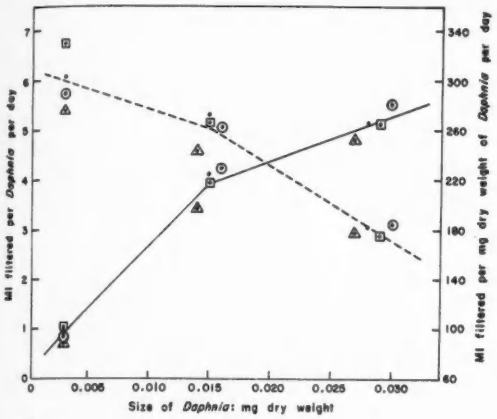

Fig. 1. The relation between size of *Daphnia* and its filtering rate at four concentrations of *Chlamydomonas*. 25,000 cells/ml •; 50,000 cells/ml ⊙; 75,000 cells/ml ⊞; 100,000 cells/ml ▲; Ml filtered per *Daphnia* ——; Ml filtered per mg dry weight of *Daphnia* – – –.

centrations used in my study and under similar feeding conditions Ryther reports filtering rates of about 1-2 ml/animal/day which corresponds to approximately 180-505 ml/mg dry wt/day calculated according to the size given. This is very close to the range of 176-330 ml/mg dry wt/day for *Daphnia pulex*.

Much work has been done on the filtering rates of marine zooplankton. Most of this work has been done on *Calanus finmarchicus* by Fuller & Clarke (1936), Harvey (1937), Fuller (1937), Raymont & Gross (1942), Gauld (1951), and Marshall & Orr (1955a, 1956a, 1956b) and has been reviewed by Riley *et al.* (1949), Gauld (1951), Ryther (1954b), Jorgensen (1955), and Marshall & Orr (1955b). Many of these workers and others (Lucas 1936; Fleming 1939; Harvey 1942; Riley 1946, 1947) have concluded that the filtering rate of the marine zooplankton studied is independent of food concentration.

Conover (1956) reported a lower grazing rate for *Acartia clausi* and *A. tonsa* at the highest phytoplankton concentration in experiments covering a range of cell concentrations of two orders of magnitude. Ryther (1954b) showed an inverse relationship between the filtering rate of *D. magna* and food concentrations below 0.15 million cells and indicated that phytoplankton age and concentration had an effect upon the feeding of this cladoceran.

An increase in filtering rate with size was reported by Gauld (1951) using several marine copepods, by Ryther (1954b) with *D. magna*, and by Marshall & Orr (1956a) on young stages of *Calanus*. The filtering rates of *Pseudocalanus minutus*, *Temora longicornis*, and *Centropages hamatus* (Gauld 1951) averaged 4.28, 8.38, and 12.99 ml/animal/day respectively and the range of filtering rates for young stages of *Calanus* (Marshall & Orr 1956a) was 1-9 ml/animal/day, the volume filtered in both investigations increasing with size. Weights were not given for these copepods but they are in the same size range as the *Daphnia* studied. These values are comparable to the range of 0.83-5.53 ml/animal/day for *Daphnia pulex*.

ENERGY OUTPUT

Oxygen consumption. The rate of oxygen consumption per animal increases with increases in body size but on a unit weight basis the rate of oxygen uptake is higher in the smaller animals (Table 5). Animals larger than 1.0 mm show a relatively constant rate of oxygen consumption per unit weight, the mean being 7.21 µl/mg/hr.

Although many difficulties were encountered with the Warburg method, oxygen consumption values obtained thereby (Table 6) compared well with those in Table 5. The similarity in the results of the two methods is further shown in Fig. 2, where the results of both methods are plotted against the dry weight of the animals. Allee & Oesting (1934) indicated the possibility of falsely high values for oxygen content due to nitrite interference when using the unmodified Winkler method for determining the oxygen content of the water. The agreement between the results of the water bottle method and the Warburg method suggests that nitrite interference, if present, was not significant.

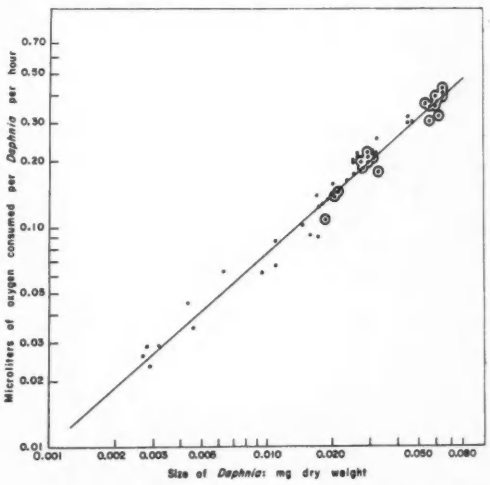

Fig. 2. The relation between the size of *Daphnia* and its rate of oxygen consumption on a double logarithmic scale. Warburg method ⊙; water bottle method •.

The data of Tables 5 and 6 show a constant relationship between relative change in oxygen consumption per animal per hour and relative change in body weight, illustrated by the double log plot in Fig. 2. This relationship may be expressed by the equation:

$$O_2 = aW^k \quad \text{or}$$

$$\log O_2 = \log a + k \log W$$

in which O_2 is oxygen consumption in micro-liters per animal per hour, W is body weight in mg, a is the intercept and k is the slope (Weymouth *et al.* 1944). Other authors have used the same equations with

TABLE 5. Oxygen consumption, carbon dioxide production, and the respiratory quotient of fed *Daphnia* as measured by the water bottle method.

Length (mm)	Dry wt (mg)	O_2 Consumption		CO_2 Production		R. Q.
		(µl/*Daphnia*/hr)	(µl/mg/hr)	(µl/*Daphnia*/hr)	(µl/mg/hr)	
0.646	0.0027	0.0262	9.704	0.0259	9.593	0.99
0.642	0.0028	0.0276	9.718	0.0285	10.018	1.03
0.642	0.0029	0.0231	7.966	0.0256	8.827	1.11
0.745	0.0031	0.0284	9.161	0.0275	8.871	0.97
0.850	0.0043	0.0457	10.630	0.0502	11.674	1.10
0.978	0.0046	0.0352	7.652	0.0363	7.891	1.03
1.011	0.0063	0.0631	10.016	0.0599	9.508	0.95
1.190	0.0095	0.0630	6.632	0.0693	7.295	1.10
1.077	0.0110	0.0674	6.127	0.0667	6.064	0.97
1.110	0.0110	0.0875	7.955	0.0813	7.391	0.99
1.318	0.0144	0.1030	7.153	0.0958	6.653	0.93
1.310	0.0160	0.0937	5.856	0.0956	5.975	1.02
1.445	0.0170	0.1419	8.347	0.1333	7.841	0.94
1.480	0.0170	0.0913	5.371	0.0875	5.147	0.96
1.420	0.0170	0.1229	7.229	0.1292	7.600	1.05
1.560	0.0177	0.1261	7.124	0.1382	7.807	1.10
1.513	0.0189	0.1345	7.116	0.1235	6.534	1.11
1.520	0.0200	0.1592	7.960	0.1463	7.315	0.92
1.620	0.0230	0.1638	7.122	0.1653	7.187	1.01
1.740	0.0250	0.2024	8.094	0.2286	9.144	1.13
1.682	0.0250	0.2021	8.084	0.2506	10.024	1.24
1.710	0.0250	0.1747	6.988	0.1764	7.056	1.01
1.750	0.0260	0.2110	8.115	0.1943	7.473	0.92
1.750	0.0260	0.2186	8.408	0.2046	7.869	0.94
1.740	0.0270	0.1835	6.796	0.2079	7.700	1.13
1.775	0.0304	0.2150	7.072	0.2365	7.780	1.10
1.820	0.0304	0.2186	7.191	0.2155	7.089	0.99
1.871	0.0320	0.2212	6.913	0.2117	6.616	0.96
1.850	0.0320	0.2568	8.025	0.3094	9.669	1.21
1.610*	0.0440	0.3261	7.411	0.3447	7.834	1.06
1.610*	0.0450	0.3002	6.671	0.2942	6.538	0.98
1.610*	0.0460	0.3033	6.593	0.2890	6.283	0.95

*Animals with six or more eggs or embryos in the brood chamber.

TABLE 6. Oxygen consumption of fed *Daphnia* as measured by the Warburg method.

Length (mm)	Dry weight (mg)	Oxygen Consumption	
		(µl/Daphnia/hr)	(µl/mg/hr)
1.45	0.0186*	0.107	5.753
1.51	0.0204	0.139	6.814
1.53	0.0210	0.142	6.762
1.75	0.0272	0.182	6.691
1.75	0.0272	0.196	7.206
1.76	0.0276	0.196	7.101
1.76	0.0276	0.201	7.283
1.76	0.0276	0.209	7.572
1.82	0.0292	0.210	7.192
1.73	0.0328	0.178	5.427
1.84	0.054**	0.365	6.759
1.77	0.056	0.357	6.375
1.74	0.057	0.306	5.368
1.71	0.059	0.360	6.102
1.97	0.061	0.378	6.197
2.01	0.061	0.400	6.557
1.77	0.062	0.326	5.258
2.10	0.064	0.407	6.359
2.10	0.064	0.402	6.281
2.22	0.064	0.417	6.516

*Weights taken from length-weight relationship (Fig. 3).
**Animals with six or more eggs or embryos in the brood chamber.

different symbols (Brody 1945; Zeuthen 1947, 1953). The regression equation fitted to the data by the least squares method is:

$$O_2 = 0.0014W^{0.881} \quad \text{or}$$
$$\log O_2 = \log 0.0014 + 0.881 \log W.$$

The value of the regression coefficient (k) has been determined for kelp crab, *Pugettia producta* (Randall), and for other crustacea from the data on oxygen consumption reported in the literature by Weymouth (1944). He calculated this value to be 0.798 for the kelp crab and 0.826 for the mean of the various crustacea taken from previous work. Benedict (1938) reports the coefficient to lie between 0.73 and 0.76 for birds and mammals. Zeuthen (1953), in a review article comparing metabolic rates of organisms ranging in size from bacteria to large mammals, shows that the value of k (b in Zeuthen's paper) is 0.7 for unicellular organisms, 0.95 for metazoa containing less than 1 mg N and 0.75 for larger poikilotherms and for homeotherms. From the respiration data of Overgaard-Nielsen (1949) on soil nematodes weighing 0.1 mg to 100 mg Zeuthen (1953) calculated a regression coefficient of 0.9. The k value of 0.881 reported here of *Daphnia* ranging in size from 3 to 46 µg is, therefore, in agreement with values

TABLE 7. Oxygen consumption of various zooplankters.

Organism	Reference	Temp. (C)	Length (mm)	Weight (mg)	O_2 Consumption (as reported)	O_2 Consumption (μl/mg/hr)*
Cladocera						
Simocephalus expinosus	Obreshkove (1930)	25	0.63	0.003[a]	5.6 cm³ x 10^{-7}/animal/min	8.40
"	"	"	1.17	0.011[a]	34.7 "	14.20
"	"	"	2.18	0.039[b]	121.6 "	14.03
"	"	"	2.44	0.08[b]	166.2 "	9.35
"	"	"	2.77	0.15[b]	202.8 "	6.08
"	Obreshkove and Banta (1930)	"	2.23	0.05[b]	133.0 "	11.97
Simocephalus vetulus	Obreshkove and King (1932)	"	1.71	0.026[a]	68.0 "	11.77
Daphnia longispina	Scherbakoff (1935)	20	1.64	0.022	5.36 mg/1000/day	7.09
Daphnia magna♀	MacArthur and Baillie (1929b)	22	—	0.046-0.140	0.029513 mg/gm/min[c]	0.72
Daphnia magna♂	"	"	—	0.056-0.079	0.036125 "	0.88
Chydorus ovalis	Scherbakoff (1935)	23	—	—	9.90 mg/gm wet wt/day[d]	1.59
Marine Cladocera	Zeuthen (1947)	16	—	0.006[e]	0.07-0.10 μl/μgN/hr	8.16-11.66
Copepoda						
Cyclops leukarti♂	Scherbakoff (1935)	20	0.75	0.0009	0.41 mg/1000/day	13.33
Cyclops leukarti♀	"	"	1.00	0.0035	1.48 "	12.29
Diaptomus graciloides♂	"	"	1.14	0.0065	1.89 "	8.46
Diaptomus graciloides♀	"	"	1.24	0.0123	2.59 "	6.10
Cyclops strenuus	"	"	2.31	0.0434	6.97 "	4.16
Calanus finmarchicus V	Marshall *et al.* (1935)	20	—	0.30[f]	0.61 ml/1000/hr	2.03
Centropages hamatus	Zeuthen (1947)	16	0.86	0.015[e]	0.08 μl/cop./hr	7.47
Centropages hamatus	Gauld and Raymont (1953)	17	0.88	0.015[e]	0.082 μl/cop./hr	7.13
Acartia clausi	Conover (1956)	20	—	0.005	8-10 μl/mg/hr	8-10
Acartia tonsa	"	"	—	0.005	12 "	12
Marine copepods	Zeuthen (1947)	16	—	0.006[e]	0.08 μl/μgN/hr	9.34

* At 20°C based on a Q_{10} of 2.0.
[a] Weight taken from length-weight relationship (Fig. 3).
[b] Weight taken from length-weight relationship of Edmondson (1955).
[c] Reported as mg Co_2 per gm per min. An R. Q. of 1.0 was assumed.
[d] Wet weight assumed to be 5.5 times the dry weight (MacArthur and Baillie 1929b).
[e] Calculated from nitrogen content assuming a protein content of 50% (Jorgensen 1955).
[f] Weight taken from Marshall et al. (1934).

previously reported for animals of the same size range and agrees with Zeuthen's conclusion that the ratio of the relative change in oxygen consumption to the corresponding change in weight is greater in small metazoa than in unicellular organisms or larger poikilotherms and homeotherms.

A comparison of the oxygen consumption of various fresh water and marine cladocerans and copepods is presented in Table 7. The rates of oxygen consumption on a unit weight basis except for *Daphnia magna*, *Chydorus ovalis*, and *Calanus finmarchicus* are in good agreement with those of *Daphnia pulex*. These exceptions are reasonable considering their larger size and the inverse relationship that exists between consumption per unit weight and weight (Weymouth *et al.* 1944; Zeuthen 1947). Many of the values given must be considered approximations since the weight of many of the organisms listed were not given but were estimated from other work, in some cases from weights of different genera or from nitrogen determinations assuming a protein content of 50% (Birge & Juday 1922; Vinogradov 1953; Jorgensen 1955). Furthermore, temperatures used varied with different workers. I used a Q_{10} value of 2.0 to express the results on the basis of 20° C. This value seems justified from the metabolic studies at different temperatures by MacArthur & Baillie (1929b), Scherbakoff (1935), Marshall *et al.* (1935), Tonolli (1947), and Gauld & Raymont (1953). Other metabolic studies of *Daphnia sp.* by Wood & Banta (1929), Fowler (1931), and Banta *et al.* (1939) and of marine copepods by Clarke & Bonnet (1939) and

Raymont & Gauld (1951) did not readily lend themselves to comparison and are not included in Table 7.

The results of oxygen consumption determinations of fed and unfed animals are shown in Table 8. It can be seen that on a unit weight basis oxygen consumption was constant in the two groups over the 6-day period. It is of interest to note the gain in weight of the fed animals and the loss in weight of the fasting animals. Kerb (1910) pointed out that after starvation the weight of Cladocera may be reduced by about 25%. After the 6-day period the daphnids lost about 50% of their weight.

TABLE 8. Comparison of oxygen consumption, carbon dioxide production, and the respiratory quotient of fed and unfed *Daphnia*.

Time (days)	Weight (mg)		O_2 Consumption (µl/mg/hr)		CO_2 Production (µl/mg/hr)		R. Q.	
	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed
0	0.027	0.023	6.796	7.122	6.660	8.037	0.98	1.13
1	0.025	0.020	6.988	7.960	7.05	7.482	1.01	0.94
2	0.025	0.016	8.084	5.856	10.019	5.095	1.24	0.87
3	0.032	0.014	6.913	7.357	6.636	6.033	0.96	0.82
4	0.030	0.010	7.072	6.127	7.768	4.473	1.10	0.73
5	0.032	0.011	8.025	7.955	9.710	5.648	1.21	0.71

Marshall *et al.* (1935) found no difference in oxygen consumption between fed and unfed *Calanus finmarchicus*. Conover (1956), however, observed a significant difference between fed and starved *Acartia clausi* and *A. tonsa*. He expressed his results on a per animal basis and therefore did not take into account a possible loss in weight by the starved animals.

Carbon dioxide production and R. Q. That the carbon dioxide production is essentially the same as the oxygen consumption for non-fasting animals is shown by the respiratory quotients which varied from 0.92-1.24 with a mean R.Q. of 1.03 (Table 5). The small variation in R.Q. as the daphnids increase in size indicates that the animal's metabolic activity does not change as it gets older under non-fasting conditions. The effect of starvation on carbon dioxide production is shown in Table 8. Like the oxygen consumption data, the carbon dioxide production of fed animals was constant during the experimental period (R.Q. = 0.96 — 1.21) but the carbon dioxide production of the unfed animals decreased. The decrease in carbon dioxide production is reflected in the R.Q. of the unfed animals which dropped from 1.13 to 0.71 during the 6-day period. This drop indicates a change in the animals' metabolism from carbohydrate utilization to protein and fat utilization.

Little work has been done on the carbon dioxide production of zooplankton. MacArthur & Baillie (1929b) reported the carbon dioxide production of male and female *Daphnia magna* to be 0.036125 mg/gm/min and 0.029513 mg/gm/min respectively at 22°C. This corresponds to 1.103 µl per mg per hour and 0.901 µl per mg per hour for males and females. These values are considerably lower than those reported in my study, but as mentioned earlier, *D. magna* is considerably larger than *D. pulex* and one would expect its metabolic activity per unit weight to be less.

Energy Utilization for Growth

Calorific Value of Daphnia. There is no significant difference between the mean values of 4059 cal/gm of the 0.7 mm group and 4124 cal/gm of the 1.3 mm group (Table 9). The mean calorific content of the 1.8 mm *Daphnia* of 5075 cal/gm, however, is significantly different from the other two size groups. The variability in calorific content within a size group was relatively constant from one group to the next as shown by the coefficients of variability which varied less than 1% between the three groups of animals analysed.

TABLE 9. Calorific value of *Daphnia* in calories per gram of dry weight.

Analysis	Mean Length of *Daphnia* (mm)		
	0.7	1.3	1.8
1	4380	4308	5075
2	4050	3926	5004
3	4044	3837	5175
4	3757	4451	5265
5	4138	4122	5281
6	3985	4097	4648
Mean	4059	4124	5075
Std. dev.	203	229	235
Coef. of var.	5.0%	4.4%	4.6%

The 0.7 mm *Daphnia* consisted of first and second instars and the 1.3 mm animals were in the last preadult instar stage which in this species is either the fourth or the fifth instar. These two groups consisted of animals without eggs or embryos in the brood chamber. The 1.8 mm daphnids were adult animals with either fully developed ovaries or with brood chambers filled with eggs or embryos.

The average increase of about 1000 cal/gm in the adult group as compared with the two immature groups indicates a change in the relative amounts of the organic constituents of the *Daphnia*. Berg (1931) observed a large number of fat globules in the ovaries and embryos of parthenogenetic *Daphnia cucullata* and *D. longispina*. Birge & Juday (1922) determined the percentage of fat in *Daphnia* and found that those animals in an active stage of reproduction and carrying many embryos in their brood chambers had a fat content of about 21% of the dry weight, whereas immature individuals or adults with few embryos yielded about 3.9% fat. Although I did not make fat analyses, the results of Berg, and Birge & Juday indicate that the larger calorific content of the adult *Daphnia* may have been due to a greater proportion of fat in these animals because of the presence of developed ovaries, egg, and embryos.

Birge & Juday (1922) determined by chemical analysis the percentages of organic and inorganic

components in various planktonic organisms in a number of Wisconsin lakes. Although they did not distinguish mature from immature forms it can be assumed from their earlier discussion that the *Daphnia pulex* samples with a low ether extract fraction represent immature *Daphnia* and those with a high ether extract fraction represent actively reproducing animals. The average percentage of carbohydrate, fat, and protein for immature *Daphnia pulex* was 27%, 4% and 47% respectively. The animals with a high fat content contained 21% carbohydrate, 20% fat, and 46% protein. From these values I calculated the calorific content of immature *Daphnia* to be 4141 cal/gm dry weight and for reproducing animals to be 5350 cal/gm dry weight. These results agree well with the values in Table 9. Ivlev (1935) compared the calorific value of Cladocera determined by an oxidation method with dichromate to that determined by means of a bomb combustion method. The results were 4447 cal/gm dry weight for the former method and 4644 cal/gm dry weight for the latter both comparing closely with the results of my study (Table 9).

Length-weight relationship. The relation between the length and dry weight of parthenogenetic *Daphnia* without eggs in the brood chamber is given in Fig. 3.

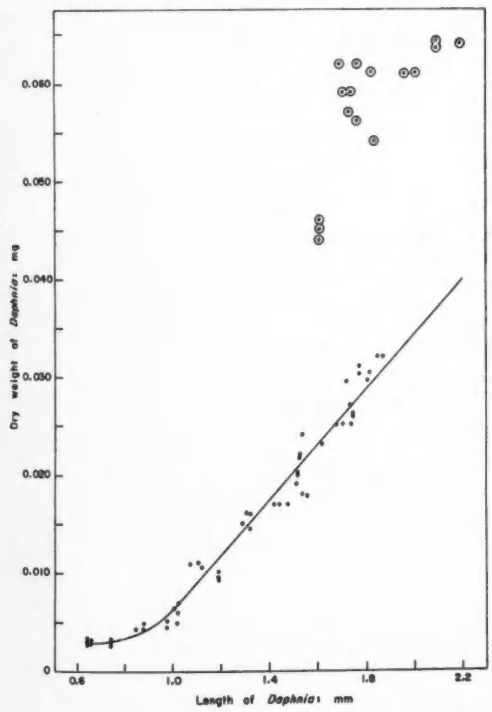

Fig. 3. The relation between length of *Daphnia* and its weight. Animals without eggs, •; animals with eggs or embryos ⊙.

The relationship is a linear one when the data for animals between 0.642 mm and 0.745 mm in length are excluded. Animals within this length range did not show variations in weight. The regression line calculated by the method of least squares for the weight of animals ranging in length from 0.850 mm to 1.871 mm can be expressed by the equation:

$$W = 0.028L - 0.022$$

where W is the dry weight in milligrams and L is the length in millimeters. The weights of the 0.642-0.745 mm *Daphnia* in Fig. 3 were connected to the fitted line by eye. The data of adult animals with eggs or embryos in the brood chamber are included on the same graph and, as would be expected, do not fall onto the line fitted to animals with empty brood chambers. These animals weighed about twice as much as animals of the same length with empty brood chambers.

A length-weight relationship for *Daphnia pulex* var. *tenebrosa* was determined by Edmondson (1955a). He found it necessary to plot the log of weight against length to get a linear relationship. The weights of *D. pulex* reported by Berg (1936) are close to those in Fig. 3.

Growth rate. Of the 7 daphnids studied at each of the four feeding levels, 5 lived through 18 instars when fed 25,000 and 100,000 *Chlamydomonas* cells/ml/day and 4 lived through this number of instars when fed 50,000 and 75,000 cells/ml/day. At all feeding levels the animals reached the 18th instar stage at the end of 40 days at which time the experiments were concluded. The average growth of the *Daphnia* which lived for 18 instars in terms of increase in total body length exclusive of spine is given in Fig. 4. The rates of growth were essentially the same at the four feeding levels up to the 8th day. After this time the growth rapidly leveled off with the average maximum length at the end of the experimental period being dependent on the food level. The average maximum length of groups fed 100, 75, 50, and 25 thousand cells/ml/day was 2.352, 2.240, 2.083, and 1.924 mm respectively. The percentage increase in average maximum length in relation to the maximum length of the 25,000 cells per ml group is 8.3%, 16.4%, and 22.3% for the 50, 75, and 100 thousand cells/ml food groups respectively. This indicates that animals fed 100,000 cells/ml/day were probably fed in excess since the percentage increase at this food level is not proportional to that at the lower food levels.

The growth of *Daphnia pulex* has been studied by Anderson *et al.* (1937) and Edmondson (1955a); *Daphnia longispina* by Ingle *et al.* (1937), Dunham (1938) and Banta *et al.* (1939); and *Daphnia magna* by MacArthur & Baillie (1929a), Anderson (1932), and Anderson & Jenkins (1942). All of these workers except MacArthur & Baillie gave the growth rate in terms of size of instars. I did not do this since it was of primary interest to determine the growth per unit of time and although in previous work adult instars have been considered as equivalent physiological time units they were not equally spaced in time (Anderson 1937). The general form of the growth curve is similar to that found by previous work and the growth curve of the *Daphnia* fed 100,000 cells/ml/day is

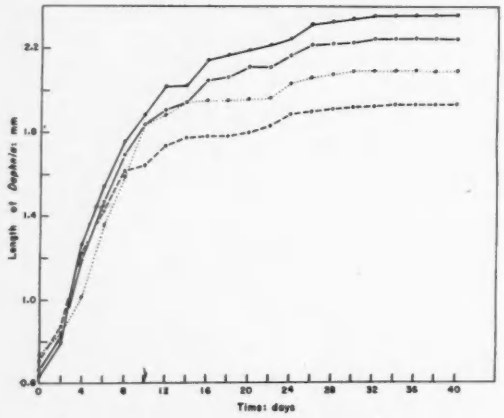

Fig. 4. Growth curves of *Daphnia* fed at four concentrations of *Chlamydomonas*. 100,000 cells/ml ——; 75,000 cells/ml ——; 50,000 cells/ml ——; 25,000 cells/ml ——.

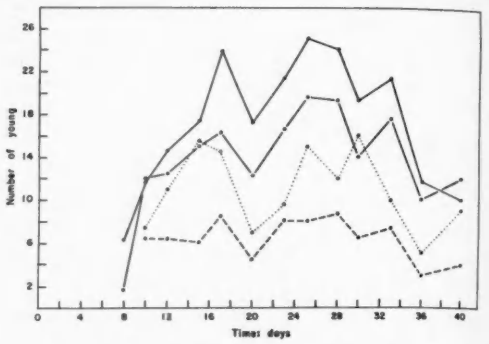

Fig. 5. Average number of young produced by *Daphnia* fed at four concentrations of *Chlamydomonas*. 100,000 cells/ml ——; 75,000 cells/ml ——; 50,000 cells/ml ——; 25,000 cells/ml ——.

practically identical with the curve of *Daphnia pulex* fed in excess by Anderson *et al.* (1937).

The effect of restricted feeding on the growth of *Daphnia* has been studied by Ingle *et al.* (1937), Dunham (1938), and Banta *et al.* (1939). These workers similarly found that poorly fed animals in corresponding instars attained sizes below those of well-fed individuals. However, the present experiments are the first quantitative studies of the effect of food supply on the growth of individual *Daphnia* since other studies have been done with a complex manure infusion medium. It is of interest to note that those animals at low food concentrations maintained a constant size during the last 12 days of the experiments.

Reproduction. Of the *Daphnia* which lived through 18 instars all were primiparous during the 5th or 6th instar and showed no apparent relation between the first appearance of eggs in the brood chamber and food supply. Accordingly, in this species there are 4 or 5 pre-adult instars. This agrees with the results of Anderson *et al.* (1937). The average number of young released during the 40-day period is given in Fig. 5. The first batch of eggs degenerated in the groups fed at 25,000 and 50,000 cells/ml and the first brood of young was released two days later than in the animals fed at the two higher food concentrations. The relation between the average number of young produced and age is remarkably similar at the three highest feeding levels, the difference being only in the levels of the curves and not in their shapes. At these three feeding levels the average number of young per brood increased for the first few broods, then an irregular but relatively high average production of young followed, and finally, the last few broods showed a rapid drop in numbers of young produced. The lowest fed group (25,000 cells/ml) produced the least number of young per brood and showed the same general trends as the three higher ones, but the variations from brood to brood were considerably less. A similar decrease in production of young with restricted feeding was reported by Dunham (1938) and Green (1954). Pratt (1943), Frank (1952), Slobodkin (1954) and Slobodkin & Richman (1956), studying the population dynamics of *Daphnia,* showed population size to be limited by food supply.

In general the curve showing the relation between the average number of young produced and the age of the *Daphnia* is in agreement with previous workers (Anderson *et al.* 1937; Dunham 1938; Anderson & Jenkins 1942; Green 1954). All of these workers except Green, however, observed a rapid decrease in the number of young produced after an initial peak. Only Green used fixed concentrations of green algae; the other workers used a manure-soil medium. His results closely resemble those in Fig. 5 where the middle instars showed a high young production before dropping off. Anderson *et al.* (1937) showed that *D. pulex* produced a maximum of 26 young/brood and the number of young subsequently leveled off to about 17 in the last 6 instars when fed manure-soil medium in excess. This agrees with the number of young produced in my study when the *Daphnia* were fed *Chlamydomonas* at a concentration of 100,000 cells/ml/day.

DISCUSSION

Ivlev (1939a, 1945), after Terroine, used the following equation to express the transformation of energy within an organism:

$$Q = Q' + Q_R + Q_t + Q_v + Q_w \qquad (1)$$

where Q represents the quantity of energy which the organism consumes as food, Q′ the energy accumulated in growth, Q_R the energy in the material egested or that energy not utilized, Q_t the energy of primary heat, Q_v the energy of external work, and Q_w the energy of internal work. Ricker (1946) indicates that Q_t, Q_v, and Q_w can be combined as respiration and this parameter represents the total energy used in the normal course of an organism's daily activities. With this modification the equation can be written as follows:

Input = Growth + Respiration + Egestion (2)

when each quantity is given in terms of energy units or calories. Lindeman (1942) makes use of the equation:

Assimilation − growth = respiration or,
Assimilation = growth + respiration (3)

Equations (2) and (3) were used in the formation of an energy budget for *Daphnia*.

The quantity of energy consumed was calculated from the filtering rate data (Fig. 1) and the calorific value of *Chlamydomonas* (1.308×10^{-6} cal/cell). At each food concentration the length of the daphnids at 2-day intervals was determined from Fig. 4 and converted to weight by means of the length-weight relationship (Fig. 3). From this weight against time relationship, the average weight for each 2-day period was converted to filtering rate (Fig. 1) and the calorific value of the algal cells consumed during each 48-hr period throughout the 40 days of growth was calculated.

The heat production was calculated by the method of indirect calorimetry using the data of oxygen consumption and R.Q. (Table 5, Fig. 2). The average weight for each two day period was converted to the rate of oxygen consumption (Fig. 2) and the calorific equivalent of the quantity of oxygen used during that time was calculated. Assuming a non-protein R.Q. of 1.0, the calorific value of 1 µl of oxygen was taken to be equivalent to 0.005 cal.

Swift & French (1954) point out that the calorific value of one liter of oxygen varies about 7% over a range of R.Q. values of 0.707-1.00 (4.686-5.047 cal l) whereas the calorific value of carbon dioxide varies about 30% (6.629-5.047) over the same range. The use of oxygen consumption values rather than carbon dioxide values for heat production calculations are, therefore, more acurate, especially since in my study measurements of nitrogen excretion were not made and the non-protein R.Q. was estimated. Swift & French also indicate that heat production values will not be very different (about 1.5% higher) when the total R.Q. and oxygen consumption data are used in the computations in place of the non-protein.

The energy accumulated in growth was calculated by converting increases in biomass to calories. The average calorific content of the pre-adult animals was considered to be 4.092 cal/mg, the average of the 0.7 mm and 1.3 mm groups. The calorific value of the adult animals was taken to be 5.075 cal/mg (Table 9). The energy of the young was calculated by totaling the average number of young per brood during the reproductive life of the animal and converting this to calories using 0.003 mg as the average weight of a newborn daphnid (Fig. 3) and 4.092 cal/mg as the calorific value. This calorific value was the mean of the 0.7 and 1.3 mm animals (Table 9).

The energy assimilated by pre-adult daphnids was computed as the sum of the energy of growth and the energy of respiration (equation 3). The energy assimilated by adult animals was calculated by taking the sum of the energy of growth, energy of young and the energy of respiration. The quantity of energy egested, which included the energy of the material not absorbed by the gut as well as that of the feces and urinary excretion, was determined by difference. The energy budget of the *Daphnia* at the 4 food concentrations was determined for the first 6 days of growth, the time required to reach the last pre-adult instar. This was also done for the last 34 days of growth during which time the animals were actively reproducing adults which developed through 13 instars and produced 13 broods of young.

The energy budget of the pre-adult *Daphnia* shows the effect of varying the concentration of food on energy transformation (Table 10). Although the energy taken up during this period increased proportionately with the available food, the energy of growth was practically constant. Similarly, the calories lost in respiration were also essentially constant. That the filtering rate and rate of oxygen consumption are independent of the concentration of algae has already been indicated (Tables 4, 8). There is, however, a direct relationship between energy consumed and energy egested. This is also shown by a 3.6 fold decrease in assimilation from 23.88% to 6.60% as the energy consumed increased from 0.469 cal to 1.910 cal or 4.1 fold. In *Daphnia*, therefore, the work involved in obtaining *Chlamydomonas* was the same at the four concentrations of food employed but the percentage of algae absorbed by the gut increased as the food concentration decreased. Ryther (1954b) pointed out that *D. magna* defecates green masses of undigested algae at high algal concentrations and suggested that the cells pass through the intestine so rapidly that the efficiency of digestion and subsequent assimilation was greatly reduced.

The efficiency of growth may be expressed as the percentage of the energy consumed that is turned into new protoplasm or the percentage of energy assimilated that is turned into new protoplasm. The former has been called the energy coefficient of growth of the first order and the latter, the energy coefficient of growth of the second order (Ivlev 1938, 1939a, 1939b, 1945; Ricker 1946). The first ratio is also referred to as the gross efficiency and the second,

TABLE 10. Energy budget of pre-adult *Daphnia* after the first six days of growth at four concentrations of *Chlamydomonas*.

Food conc. (cells/ml/day)	Energy consumed (cal)	Energy of growth (cal)	Energy of resp. (cal)	Energy of egestion (cal by diff.)	% Assimilation	% Energy consumed as growth	% Energy assim. as growth
25,000	0.469	0.062	0.050	0.357	23.88	13.22	55.36
50,000	0.582	0.053	0.039	0.490	15.81	9.11	57.61
75,000	1.388	0.066	0.050	1.272	8.36	4.76	56.90
100,000	1.910	0.074	0.052	1.784	6.60	3.87	58.64

TABLE 11. Energy budget of adult *Daphnia* after thirty-four days of growth at four concentrations of *Chlamydomonas.*

Food conc. (cells/ml/day)	Energy consumed (cal)	Energy of growth (cal)	Energy of resp. (cal)	Energy of egestion (cal by diff.)	% Assimilation	% Energy consumed as growth	% Energy assim. as growth
25,000	5.671	0.071	0.791	3.872	31.72	1.25	3.95
50,000	13.004	0.101	0.902	10.381	20.17	0.78	3.85
75,000	19.351	0.111	0.970	16.093	16.84	0.57	3.41
100,000	27.328	0.116	1.032	23.442	14.22	0.43	2.99

the net efficiency, of growth. The gross efficiency of the pre-adult *Daphnia* decreased from 13.22% at the lowest food concentration to 3.87% at the highest. The percentage of the energy assimilated that went into growth, however, was practically constant at the four food concentrations ranging from 55.36% to 58.64%. Thus, the pre-adult animals assimilated practically the same amount of food at each food concentration, whereas, the amount egested increased approximately in the proportion in which the available food increased.

In the adult animals the energy of growth increased with increasing food, but, as in the pre-adults, the energy egested also increased and the percentage of food assimilated decreased (Table 11). The gross and net efficiencies do not include the energy of young and, as would be expected, are close to zero since growth was very small (Ivlev 1945; Ricker 1946). The energy of the young produced during this period was not included in Table 11 in order to show the decrease in efficiency of food conversion into individual growth with age. This energy budget, therefore, is not balanced.

The major portion of stored energy in the adults went into the production of young (Table 12). Again the inverse relationship between food consumed and gross efficiency is evident (16.52%-10.2%). The net efficiency of the production of young, however, increased from 52.08% at the lowest food concentration to 70.46% at the highest. This increase in net efficiency with higher food concentrations can be explained by noting that the calories assimilated by the adults equal the sum of the energy of adult respiration, the energy of adult growth, and the energy of the young produced. Since the increase in the energy of growth plus production of young in the adults is greater with increasing food than is the energy of respiration, this efficiency would necessarily increase as the food consumed increased. Since the energy of adult growth is not included in Table 12 this energy budget like that of Table 11 is not balanced.

TABLE 12. Efficiency of reproduction by *Daphnia* fed at four concentrations of *Chlamydomonas.*

Food conc. (cells/ml/day)	Avg. no. of young produced	Energy consumed (cal)	Energy of young (cal)	Energy of resp. (cal)	% Energy consumed as young	% Energy assimilated as young
25,000	76.3	5.671	0.937	0.791	16.52	52.08
50,000	132.0	13.004	1.620	0.902	12.46	61.76
75,000	177.2	19.351	2.177	0.970	10.94	66.82
100,000	223.0	27.328	2.738	1.032	10.02	70.46

The energy budget of the pre-adult and adult animals and the energy involved in reproduction can be combined to show the energy balance of *Daphnia* after 40 days of growth or after 18 instars (Table 13). Since the major portion of stored energy went into the production of young, the efficiencies do not change very much from those in Table 12. This was also implied by the constancy of R.Q. throughout the life of the daphnids (Table 5). The gross efficiency of growth decreased from 17.43% to 10.01% with increased algal consumption, whereas the net efficiency of growth increased from 55.99% to 72.98%.

TABLE 13. Energy budget of *Daphnia* after forty days of growth at four concentrations of *Chlamydomonas.*

Food conc. (cells/ml/day)	Energy consumed (cal)	Energy of growth and young (cal)	Energy of resp. (cal)	Energy of egestion (cal by diff.)	% Assim.	% Energy consumed as growth and young	% Energy assim. as growth and young	% Energy of growth and young as resp.
25,000	6.140	1.070	0.841	4.229	31.12	17.43	55.99	78.60
50,000	13.586	1.774	0.941	10.871	19.98	13.06	65.34	53.04
75,000	20.739	2.354	1.020	17.365	16.27	11.35	69.77	43.33
100,000	29.238	2.928	1.084	25.226	13.72	10.01	72.98	37.02

Lindeman (1942) calculated the productivities and progressive biological efficiencies of the trophic levels in Cedar Bog Lake. He did the same thing for Lake Mendota using the data of Juday (1940). According to Lindeman (1942) the productivity of a trophic level is defined as the rate of assimilation of energy into a trophic level and the progressive biological efficiency is the ratio of the productivity of one trophic level to that of the preceding trophic level. Thus the progressive biological efficiency represents the degree of utilization of energy from the previous trophic level. Since Lindeman's decomposition correction represents energy unassimilated by the next trophic level, the amount of energy taken in by the primary consumers is equal to the sum of predation and decomposition of the primary consumers which I calculated from his data to be 17.6 cal. Similarly the amount of energy passed on to the secondary consumers is equal to the sum of predation and decomposition of the herbivores which was calculated to be 3.4 cal. The ratio of primary consumer yield to intake according to Lindeman's data is, therefore, 3.4 to 17.6 or 19.3%. For Juday's data, following Lindeman, this ratio is 2.6 cal to 52 cal or 5.0%. These percentages are comparable to the gross efficiency of growth of *Daphnia* (Table 13). Dineen (1953) calculated the efficiency of primary consumers to be 18.4%. This, however, is a progressive efficiency in Lindeman's sense and not strictly comparable to the gross efficiency of growth.

It should be pointed out that Lindeman used Ivlev's data (1939b) on *Tubifex* to correct for energy lost in respiration. This correction factor was the ratio of respiration to growth. Since the *Tubifex* in Ivlev's experiments were actively growing (as shown by a 100% increase in biomass after the 24 days of the experiments) the respiratory correction estimate of 62.3% by Lindeman is at best a rough approximation. At that time, however, no other data were available. The same correction factor calculated on the basis of 40 days of growth in *Daphnia* was 78.60% to 37.02% depending on food concentration (Table 13). In the case of *Daphnia*, therefore, where respiration is independent of the food consumed, this correction factor will decrease with increasing food consumption since the energy of growth and reproduction are directly related to the amount of energy consumed.

Ivlev (1939a) determined the energy coefficient of the first order (gross efficiency) to be 31.6% in young *Tubifex*. In another study on the energy balance of young carp Ivlev (1939b) reported a gross efficiency of 31.3%. In both cases the animals were young and actively growing indicating that the mean efficiencies over the life span of these organisms would probably be lower. The net efficiencies were 62% for *Tubifex* and 42% for the carp. Ricker (1946), summarizing the available data, reports the gross efficiencies based on weight increases of various fishes fed on natural food to range from 10% to 36% depending on the age and the amount of food consumed. It should be noted, however, that efficiencies based on weight increases are not strictly comparable to efficiencies based on energy transformations. Odum (1957) calculates the ecological growth efficiency (gross efficiency) of the herbivores of Silver Springs, Florida to be 44%. Brody (1945) estimates the gross efficiency of growth of cattle to decline from 35% for early postnatal growth to 5% at two years of age. The growth efficiencies of *Daphnia* (Table 13) are in the same range as those animals mentioned above. The similarity of growth efficiencies for all animals is of considerable interest. If one considers, however, that the chemical reactions involved in intermediary metabolism are common to most organisms this constancy is not too surprising.

Considerably more quantitative data must be obtained before we will have a clear picture of aquatic community dynamics. The quantitative approach of Riley *et al.* (1949) to the dynamics of marine plankton needs to be extended to fresh water communities. Experimental studies on the energy budgets of many aquatic organisms should be undertaken and it is important that experimental techniques be adapted to measure energy relationships of organisms in their natural habitat.

SUMMARY

1. The calorific value of *Chlamydomonas reinhardi*, grown under sterile conditions, was determined with a micro-oxygen bomb calorimeter. The average calorific value was 5269 cal/gm which was equivalent to 1.308×10^{-6} cal/algal cell. The calorific value per unit weight of *Daphnia pulex* was determined by the same method and was found to change after the animals developed mature ovaries or contained eggs in the brood chamber. The average calorific value of newborn (0.7 mm), last pre-adult instar (1.3 mm), and actively reproducing animals (1.8 mm) was 4059, 4124, and 5075 cal/gm respectively.

2. *Chlamydomonas reinhardi* had an ash content of 3.94% as determined by loss after ignition and a nitrogen content of 3.95% as measured by the micro-Kjeldahl method.

3. The filtering rate at 20°C of 0.7, 1.3, and 1.8 mm *Daphnia* at 4 food concentrations was determined by differential algal cell counts from 24-hr experiments. The filtering rate was independent of the algal concentrations which were 25,000, 50,000, 75,000 and 100,000 cells/ml/day. The feeding rate increased with size in a curvilinear fashion from 0.90 ml to 5.15 ml/animal/day. On a unit weight basis the rate of filtration decreased with size.

4. Oxygen consumption at 20°C was determined by the Warburg method and the water bottle method. With the Warburg method the small volume of water caused the animals, in many cases, to get caught in the surface film. Because of this, it was felt that the water bottle method was more accurately measuring the oxygen consumption under natural conditions. In spite of this, however, the results of both methods were in agreement. The relative change in oxygen

consumption was directly related to the relative change in body weight. The regression equation of log 0_2 on body weight (W) was calculated to be:

$$\text{Log } 0_2 = \log 0.0014 + 0.881 \log W$$

The rate of oxygen consumption per unit weight was higher in small animals. *Daphnia* larger than 1.0 mm showed a relatively constant rate of oxygen consumption per unit weight, the mean being 7.12 μl/mg/hr. The oxygen consumption of fed *Daphnia* was compared to that of animals starved 1-5 days. On a unit weight basis oxygen consumption was constant in the two groups during this time.

5. Carbon dioxide production was determined by measuring pH changes in the same experimental bottles was used in the oxygen measurements. Carbon dioxide production of fed *Daphnia* was found to be the same as the oxygen consumption. The respiratory quotients ranged from 0.92 to 1.24 with a mean R.Q. of 1.03. The carbon dioxide production of unfed animals decreased with the length of starvation. The respiratory quotients of fasting animals dropped consistently after each additional day of starvation. The total change in R. Q. during 5 days of starvation was from 1.13 to 0.71.

6. The length-weight relation of *Daphnia* was determined and found to be linear for animals ranging in length from 0.9 mm to 1.9 mm. The regression line of weight on length was calculated to be:

$$W = 0.028\ L - 0.022$$

where W was the dry weight in milligrams and L the length in millimeters. Animals ranging in length from 0.64 to 0.75 mm did not show a gain in weight. *Daphnia* with eggs or embryos in the brood chamber weighed about twice as much as animals of the same length with empty brood chambers.

7. Growth and reproductive rates were determined at 20°C for 40 days at the 4 food concentrations previously mentioned. During this time animals at each food level lived through 18 instars and produced 13 broods of young. During the first 8 days the growth rates at the 4 food concentrations were almost the same. After this time the amount of growth increased with food. The average length at the end of the growth experiments of groups supplied with 100,000, 75,000, 50,000 and 25,000 cells/ml/day was 2.352, 2.240, 2.083, and 1.924 mm respectively. Animals were primiparous during the fifth or sixth instar regardless of food level. The average number of young per brood increased with feeding; the average total number of young was 223.0, 177.2, 132.0, and 76.3 arranged in order of decreasing food supply.

8. An energy budget for pre-adult animals was constructed at each food concentration following the equations:

$$\text{Input} = \text{Growth} + \text{Respiration} + \text{Egestion}$$
$$\text{Assimilation} = \text{Growth} + \text{Respiration}$$

each quantity being expressed in terms of energy units. The energy of growth for the pre-adults was practically constant at the 4 food levels as was the energy respiration. As the food consumption of the pre-adults increased the energy of egestion also increased and the percentage assimilated decreased. The gross efficiency of growth decreased from 13.22% to 3.87% as the food supply increased. The net efficiency of growth was essentially constant at the 4 food levels (55.36-58.64%).

9. A similar energy budget was constructed for the adult animals. The gross efficiency in older *Daphnia* ranged from 1.25 to 0.43% and the net efficiency ranged from 3.95 to 2.99%.

10. The major portion of stored energy in the adults went into the production of young. The gross efficiency of young production decreased with food from 16.52% to 10.02%. The net efficiency of young production increased with food from 52.08% to 70.46%.

11. Combining the energy relationships of the pre-adults and adults, a total energy budget of *Daphnia* is presented for 40 days of growth. A discussion is given of some of the published work on energy relationships in other organisms and in aquatic communities.

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